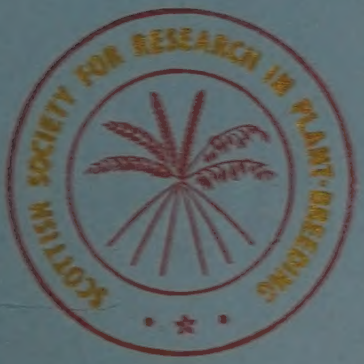
# SCOTTISH PLANT BREEDING STATION




# REPORT
## 1959

22 MAY 1959

(*a*)

(*b*)

(*c*)

BREEDING FOR RESISTANCE TO POTATO ROOT EELWORM

# PLATE

## Breeding for Resistance to Potato Root Eelworm

Resistance is a heritable character. An important feature of resistant plants is their ability to stimulate the hatching of eelworm larvae from cysts present in the soil, and although the plants themselves are susceptible to eelworm attack the invaders are incapable of reproduction in the roots. The action of a resistant potato variety is, therefore, to mop-up eelworm and consequently to reduce the eelworm content of infested soils.

(*a*) A plot of Kerr's Pink. The area in foreground had been occupied by a non-resistant variety the previous year, and that in the background by an eelworm resistant one. The more vigorous crop closing the drills (background) illustrates the extent to which the eelworm population in the soil has been reduced.

(*b*) From left to right, diploid, tetraploid and octoploid forms of *Solanum vernei* subsp. *ballsii*, an eelworm resistant diploid species from Argentina reputed to be frost resistant. The tetraploid crosses easily with commercial potato varieties.

(*c*) A tetraploid form of *Solanum sanctae-rosae*. Another Argentinian diploid eelworm resistant species which is also reputed to be frost resistant. The tetraploid can be crossed with commercial varieties but the fertility is reduced.

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SCOTTISH PLANT BREEDING STATION

PENTLANDFIELD, ROSLIN, MIDLOTHIAN

# REPORT

## 1959

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## DIRECTOR'S REPORT

**Cereals.**—The breeding of oat varieties suitable for Scottish conditions has once again been the main preoccupation of the Cereal Section. To this end, selections from unfixed hybrid material were made in three separate environments, in Argyll, in Inverness-shire, and at Pentlandfield.

The value of making selections in the environments for which the new varieties are intended has been demonstrated by a series of trials at Pentlandfield in 1958 in which 96 fixed lines, derived from 13 different hybrids by selection at the three centres, were tested against a control variety, Sun II. It is particularly noticeable that at Pentlandfield only one line from the Argyll centre gave a yield equal to that of the control whereas the control was equalled or bettered by 21 lines selected in Inverness-shire, or at Pentlandfield. Not only was this so, but in almost every case where related lines were derived from the same hybrids those which originated at the West centre produced lower yields than sister lines from the other two centres.

When it is remembered that grain yield was the principal basis of selection in each environment, it becomes apparent that a variety which is relatively high yielding in Argyll will not generally be of a type likely to yield well in the drier and more fertile environments of the East. Trial experience has already shown that the converse is true, high yielding varieties of the Sun II type being unsuited to the Argyll locality.

Selection for resistance to oat stem eelworm has continued, between 20,000 and 30,000 seedlings having been inoculated with a suspension of eelworm. The hybrid material used in these experiments has included second and third backcrosses to commercial types, and a number of useful resistant lines have been obtained which should shortly be ready for multiplication and testing on a field scale.

**Herbage Plants and Genecology.**—The importance of hill grazings to agriculturists has been emphasised recently by the fact that the problems involved in their improvement have been discussed at a series of meetings and conferences arranged by different bodies and societies throughout the country. The genecological investigation of hill species continues and though no breeding programme is at present envisaged, the

range of variation within certain species is being investigated. As mentioned in previous reports, a considerable amount of work has been done on the *Festuca ovina* complex and some results have also been obtained for two hill species, *Agrostis tenuis* and *A. canina*. Tillers of these grasses were collected from nearly all the 226 populations sampled in 1957 and are being grown in a random lay-out suitable for statistical analysis of the data obtained from the individual plants. Before, however, any analysis could be attempted, it was necessary to identify accurately the species or, in the case of *Festuca ovina* (sens. lat.), the chromosome race of each plant and this work has occupied a considerable amount of time. The large majority of the 226 populations sampled were in South East Scotland and as this is a region within which both chromosome races of *Festuca ovina* are known to occur (see abstract of paper on page 22) the chromosome number of some 1,600 plants had to be counted since morphological characteristics are inadequate or misleading. The results are in themselves of considerable interest.

In the main area most of the plants were either diploid or tetraploid, but seven triploids, one hexaploid, two aneuploids and eight plants with B chromosomes were found. Based on counts of up to eight plants, 194 populations from South East Scotland can be classified as follows : diploid, 37 ; tetraploid, 123 ; mixed, 34. Most of the mixed populations were composed of predominantly one race or the other : of the 27 mixed populations in which eight plants have been counted, 16 have been classified as mixed although only a single plant of one of the races was present. The sites from which the populations were gathered can mostly be classified into the following botanical categories :—

| | |
|---|---|
| Species rich Bent-fescue | Community type A |
| Species poor Bent-fescue | ,, ,, B |
| *Nardus* dominated | ,, ,, C |
| *Calluna* ,, | ,, ,, E |
| *Molinia* ,, | ,, ,, D |

The distribution of diploidy or tetraploidy within this scheme indicates an ecological difference between the two races.

| Community type | A | B | C | E | D |
|---|---|---|---|---|---|
| Tetraploid plants | 340 | 242 | 119 | 166 | 95 |
| Diploid plants | 8 | 12 | 61 | 130 | 177 |
| % tetraploid plants | **98** | **95** | **66** | **56** | **35** |

It should be mentioned that a further sixteen populations were collected in the North West of Scotland (nine being from bent-fescue communities) and, as was to be expected in this area, all were diploid.

The work involved in the cytological separation of the chromosome races of the *Festuca ovina* complex was considerable but conclusive whilst the difficulties encountered in distinguishing between the species in the *Agrostis* group were less easily solved for several reasons. In the first place the collected plants showed morphological characters which suggested that, in addition to *A. canina* L. subsp. *canina*, which is diploid and also easily distinguished morphologically, *A. stolonifera* L. or at least hybrids with it might be present as well as *A. tenuis* Sibth. and *A. canina* L. subsp. *montana* Hartm. No recourse to chromosome counting could be of any assistance in this case since *A. tenuis*, *A. canina* L. subsp. *montana* Hartm. and *A. stolonifera* are all tetraploid. Several morphological characteristics separate these three taxa but each has a fairly wide range of variation in itself and it is not an easy matter to decide the correct taxonomic interpretation of data when variation is considerable and is in apparently contradictory directions. The size and shape of the ligule is said to be of great value in identification but there seemed to be too many plants in which the size of the awn, for example, suggested another interpretation. It therefore seemed necessary to make as intensive an examination as possible of the *Agrostis* collection to try to find some character upon which to place most weight in identification. In previous trials which contained only two *Agrostis* taxa, it had been found helpful to obtain more data by examining the floral characters under a microscope and this was carried out for over 600 of some 1,600 plants. Measurements were taken for lengths of ligule, awn, lemma, palea, anther, and where available, seed; for the degree of hairiness of glume 1 and at the foot of the lemma; for the number of nerves on the lemma: earlier in the season the type of ligule had been noted at time of first ear emergence. It was found that the length of the awn and the number of nerves on the lemma were variable even on occasion within a single panicle, but that the lengths of the lemma, anther, seed, showed very little variation whilst the " hairiness " characters varied at random. The measurement of the palea, however, seemed to substantiate to a large extent the identification by

ligule type even though other characters might be odd. It was found eventually that a figure representing the palea length as a percentage of the lemma gave a very good separation of *A. tenuis* Sibth. from *A. canina* L. subsp. *montana*.

| Palea length as % of lemma | | 0–30 (" canina ") | | 30 upwards (" tenuis ") | |
|---|---|---|---|---|---|
| Identification on ligule type | | canina | tenuis | canina | tenuis |
| Nerves | 3 | 6 | 5 | 2 | **211** |
| on | Number varying within panicle | 14 | 1 | 5 | 46 |
| lemma | 5 | **228** | 5 | 6 | 73 |
| | 5 upwards | 1 | 0 | 0 | 1 |
| | TOTAL | 249 | 11 | 13 | 331 |

It is interesting to note that a general observation of the size *and* shape of the ligule is much more valuable for diagnostic purposes than the measurement of its length alone for length gives no separation at all between species, but in more than 96 per cent of the plants examined, eye estimation of the ligule *type* has been confirmed by the percentage value, palea to lemma. The group of less than 4 per cent contained most of the plants which had been marked as doubtful during ligule estimation and all were re-classified on the basis of a majority of characters. It seems, therefore, that dependence upon the evidence of the flowering stem ligule type alone gives in most cases a quick and accurate identification.

The question of the presence or absence of *A. stolonifera* within the " tenuis " group remained undecided but an analysis of the 5-nerved " tenuis " types showed that the majority had awns and since the " *stolonifera* " shape of lemma had not been observed during the microscope examination, it seemed reasonable to suppose that all the " tenuis " group belong to *A. tenuis* Sibth. which must be very variable in nature. It may be that some of this variability is due to crossing and back crossing with *A. stolonifera* but plants which showed the most marked development of stolons were not sufficiently different

in other respects from *A. tenuis* to warrant separate treatment. It is difficult to find an explanation for varying numbers of nerves on lemmas within a panicle and the few plants which fall into this group will be examined for meiotic irregularity.

A table analysing the occurrence of the two *Agrostis* species within each community type shows a significant similarity to the table already given for the distribution of the two chromosome races of *Festuca ovina*.

| Community type | A | B | C | E | D |
|---|---|---|---|---|---|
| *A. tenuis* Sibth. | 324 | 187 | 83 | 55 | 24 |
| *A. canina* L. subsp. *montana* | 30 | 68 | 107 | 259 | 231 |
| % *A. tenuis* Sibth. | **92** | **73** | **44** | **18** | **9** |

The preliminary work on local *Taraxacum* indicates that within the area no single genotype has as wide an ecological tolerance as the genus, so that habitats tend to be populated by a characteristic selection of the available genotypes. Nevertheless, each genotype has a wide range of tolerance and can be found in several quite distinct habitats. It appears that selection is sufficiently strong to differentiate completely between, for instance, a dry and a water-logged habitat, but that the differentiation between different forms of marsh habitat is so slight that a very big trial would be needed to demonstrate it.

During the work on the vegetative spread of individual genotypes in natural communities a rough relationship has been noticed in that, as might be expected, vigorously creeping species tend to have the most extensive genotypes. However, the very vigorously creeping *Trifolium repens* seems to be limited to moderately small genotype patches, suggesting that the species is a short lived perennial, and further work is in progress.

The work on lead tolerance in *Festuca ovina* (sens. lat.) has now shown that the highly tolerant form is widespread in the Pennine mining areas. Those populations which appear to be medium tolerant, in fact contain mixtures of plants of high and low tolerance. This is quite different from the situation at Leadhills, where the populations are almost certainly not mixtures but pure stands of a medium tolerant form. The most interesting discovery among the Pennine material was that the two chromosome races were present and that tolerant plants could be found in both. In a few populations tolerant

plants of chromosome numbers 14, 21 and 28 were found together, and this material will be crossed in 1959 for genetic analysis.

Lead has been found to have a double action on the growing root. It inhibits cell elongation, and it also interferes with mitosis. In spite of this it is not a violent cytoplasmic poison, and mature root cells can be placed in solutions containing very high concentrations of lead without being suddenly killed. After several hours treatment with 1 per cent lead nitrate, for instance, root cap cells can be plasmolysed in sugar and allowed to recover in water in an apparently normal manner.

It is proposed to extend the work on lead tolerance to an investigation of some of the physiological mechanisms involved, and the effect of lead on the inversion of sucrose by excised root segments is now being examined. It is hoped that this may lead not only to a better understanding of tolerance but also to a more precise method of measuring it, and so to more reliable interpretations of the genetical results.

In an attempt to speed up growth and provide winter material for physiological study, 180 plants of *Festuca ovina* have been kept under continuous supplementary light in a heated greenhouse since the middle of November. 24 (13%) of these plants were shooting by the end of December and flowering by the end of January. This suggests that most plants of *F. ovina* require cold treatment before flowering in response to a long photoperiod, but that a few are able to flower without it.

A considerable amount of cytological work was carried out during the year on various species but most of the work was concerned with the *Graminae* and in particular the *Festuca ovina* group, the *F. rubra* group and *F. heterophylla*, and hybrids between them.

In addition to straightforward chromosome counting, meiosis was looked at in some plants thought likely to be most interesting—*e.g.*, in the *F. ovina* group plants with one or more B chromosomes in addition to the normal complement of 14 or 28, triploids and aneuploids, and one odd plant from the populations collected in South East Scotland with 42 chromosomes. The B. Chromosomes were very small—about $\frac{1}{3}$–$\frac{1}{2}$ the size of the normal chromosomes. At meiosis they were seen to pair only with each other, and never with chromosomes of the normal complement.

In the *F. ovina* group the diploid regularly forms seven

bivalents at meiosis ; the tetraploid forms one or two quadrivalents per cell + 10-14 bivalents ; the triploid forms an average of about 4 trivalents per cell (maximum pairing 7 trivalents) ; the hexaploid shows similar pairing to the tetraploid, 1 or 2 quadrivalents + 17-21 bivalents per cell, with an occasional association of 6 chromosomes. All the plants of *F. heterophylla* studied had 28 chromosomes and formed 14 bivalents at meiosis. In the *F. rubra* group, plants were of three different types with 2n = 42, 49 and 56 respectively. The hexaploid formed 21 bivalents at meiosis ; the heptaploid had an average of 2 or 3 trivalents and 18 or 19 bivalents per cell, and the octoploid an occasional quadrivalent and 26 or 28 bivalents per cell.

The pairing in the hybrids *F. ovina* (28) × *F. rubra* (42) and *F. ovina* (42) × *F. rubra* (42) varied a good deal. In extreme cases more than half the chromosomes regularly remained unpaired and later stages of division were very disturbed, the plants being, presumably, completely pollen-sterile. The hybrid *Lolium perenne* (14) × *F. rubra* (42) showed very low pairing at meiosis. A maximum of 4 bivalents was seen in one cell, while several cells had 28 unpaired chromosomes.

Some *Agrostis* spp. were also available for examination and samples of *A. canina* L. subsp. *montana* (2n = 28) and *A. tenuis* Sibth. (2n = 28) and hybrids between them were examined at meiosis. *A. canina* shows a maximum pairing of 5 quadrivalents and 4 bivalents whilst *A. tenuis* regularly forms 14 bivalents. All the hybrids so far examined form 14 bivalents at meiosis.

**Potatoes.**—The Registration Trials conducted by the Department of Agriculture for Scotland in 1958 contained thirteen of the Station's seedlings. Three of them were recommended for further trial in 1959, and one (Ref. No. 2151b(31)) was registered as a new variety suitable for commercial cultivation. It has been named Pentland Crown and its official description is as follows :—

Maturity : Early maincrop.

Tuber : Oval, slightly flat ; skin white turning mainly green on exposure ; flesh white ; eyes shallow to medium, those at rose end set in shallow depression ; sprouts green with faint pink colour at bases.

Foliage : Haulm of medium height to tall, bushy, stems thin, fairly numerous, green with faint pink at bases,

branching occasionally ; nodes green, swollen ; wings green, waved ; leaf average to small in size ; moderately short and narrow, open, slightly arched, midrib green ; leaflets small, light green matt, wrinkled, pointed at tips, leaflet stalks long and green ; secondary leaflets fairly numerous, cordate, small.

Flower : White, rare ; anthers orange ; inflorescence stalks short, slender ; buds green, few, berries not observed.

Remarks : Cropping very good ; cooking quality good ; keeping quality good ; fairly high resistance to Virus Y ; moderately resistant to Dry Rot and to Gangrene as tested in the laboratory (normally similar reaction in the field) ; susceptible to Skin Spot. Registered 1958.

The experimental work on breeding for field resistance to blight was continued during 1958 on an extended scale. About 140 resistant seedlings raised and tested in previous years were grown in field plots in order to assess their economic potentialties and to compare their responses to the disease under natural conditions. Although the season was particularly favourable for blight, the vast majority remained free from the disease and none was severely affected. A further series of new progenies, amounting to about 5,000 plants was raised and exposed to infection under laboratory conditions with race 1, 2, 3, 4. The majority of these progenies was found to contain a relatively small porportion of plants possessing enough field resistance to survive the test and grow to maturity. Only such plants were retained, the less resistant forms being destroyed in the course of the test. In the few remaining progenies, tested in the same manner, hypersensitives and susceptibles segregated in Mendelian fashion, indicating the action of a new R gene inducing hypersensitivity to race 1, 2, 3, 4. These hypersensitive segregates were later tested with a race of blight received from Professor Dr R. Schick, East Germany, and about half of them proved susceptible to it. Thus the existence of a fifth R gene in *S. demissum* (C.P.C. 2171) was confirmed, as was also the existence of a race of blight capable of overcoming it. This incident serves to emphasise further the vulnerable nature of hypersensitivity as a form of protection against a disease organism that has many biotypes.

Samples of blight were collected from the field plots during the growing season and classified according to the reaction to infection of the differential host series. The races found were : 4 ; 1, 4 ; 2, 4 ; 3, 4 ; and 2, 3, 4. Cultures of blight isolated

from both potato and tomato crops were also received for identification from several countries overseas. The results of the tests provided further information on the distribution of the different biotypes and their different preferences for potato or tomato.

At present, two kinds of field populations of the potato-root eelworm can be distinguished in Britain by differences in pathogenicity, although the appearance of the cysts is the same. The eelworm resistance of *S. tuberosum* subsp. *andigena* C.P.C. 1673 is effective against one kind, typified by the Boghall population at Pentlandfield, but breaks down against the other kind, typified by the Duddingston population at Pentlandfield.

Since the resistance to the Boghall population in C.P.C. 1673 was adequate for the original breeding programme, this was considered to be the " standard " level of resistance in parental material. Standard resistance consequently implies that 90 per cent of the plants infected under given conditions have root systems which remain free from cysts. A corresponding level of resistance to the Duddingston population was sought in several collections of wild potatoes during the last two years. For the purposes of this record standard or near standard resistance to both populations is called " nonspecific " if present in the same plant. " Specific " resistance was displayed by plants which had standard or near standard resistance to a specified population, but definitely less than standard resistance to the other.

The eelworm resistance of *S. vernei* subsp. *ballsii* is above standard, nonspecific and polygenic. The hybrids between tetraploid forms of this species and *S. tuberosum* were very uniform in their resistance to the Duddingston population, but the level of resistance was less than standard. Selected hybrids will be crossed together in an effort to counteract the reduction in resistance which took place in the species cross. The breeding line (subsp. *ballsii* 2n × *S. demissum* 6n) × *S. tuberosum* was discontinued because the tetraploid triple hybrids were very wild and resembled *S. demissum* in their greater susceptibility to the Boghall population.

Specific resistance to the Duddingston population was confirmed in *S. multidissectum* and *S. neohawkesii*, at a level slightly above standard in the former and slightly below standard in the latter. The segregation of seedlings with

standard resistance in the cross *S. multidissectum* (unreduced gametes) × *S. tuberosum* was suggestive of dominant, monofactorial inheritance. No such segregation occurred in the cross *S. neohawkesii* (unreduced gametes) × *S. tuberosum*. Some resistance to the Boghall population was linked with the standard resistance to the Duddingston population in *S. multidissectum*. *S. neohawkesii* was more susceptible to the Boghall population and the poorer source of resistance generally. These two species and *S. vernei* are diploid species in the series *Tuberosa*.

Resistance to the Duddingston population was also confirmed in *S. sanctae-rosae*, *S. megistacrolobum* and *S. raphanifolium*, three diploid species in the series *Megistacroloba*. The resistance was above standard and nonspecific in the first species but slightly less than standard and specific to the Duddingston population in the other two species. The resistance in *S. raphanifolium* is probably controlled by one or very few genes.

*S. famatinae* (series *Tuberosa*) differs from the other diploids in having standard resistance which is specific to the Boghall population, thus tending to interact with pathogenicity type in the way characteristic of subsp. *andigena* C.P.C. 1673.

The species which have been mentioned provide examples of the efficient types of eelworm resistance, diverse in nature and inheritance, which can be found in wild potato species. A few seedlings are not enough to characterise a species and even the names of some of the species mentioned are provisional, but already a genetic basis for certain aspects of the host/parasite relationship seems possible. The resistance in *S. multidissectum* is apparently the antithesis of that present in subsp. *andigena* C.P.C. 1673 but the breeding lines utilising these strain specific types of resistance will go forward separately until the genetics of pathogenicity type in the eelworm are better understood. Meanwhile, there is some justification for attempting to use the nonspecific resistance of subsp. *ballsii* as a background upon which to impose specific resistance, provided the latter is controlled by one or very few genes. The nonspecific resistance of *S. sanctae-rosae* is also potentially valuable, but more difficult to investigate because of reduced fertility in crosses between the tetraploid forms of this species and *S. tuberosum*.

During the summer, consignments of tuber-bearing *Solanum*

species were received from the Birmingham Plant Collecting Expedition to Mexico and Central America under the direction of Dr J. G. Hawkes. These tubers were grown under glass and the resulting plants were tested for the presence of viruses. In the course of this work, two diseases were found which were unfamiliar and it is proposed to investigate the causal viruses further. After initial multiplication, the collection will be examined for the presence of any characters which may be of value in potato breeding. It is unfortunate that the earlier consignments consisted mostly of mother tubers, as germination of these tubers was very poor and few plants were obtained. The later consignments of younger tubers are being held in store for growing in the spring when better germination should be obtained.

Genetical studies on various characters associated with resistance to viruses were continued. In progenies derived from *S. chacoense*, resistance to virus Y is manifested in two forms—a null reaction and a necrotic, hypersensitive reaction. Segregation data obtained during the year suggest that the two forms of response are controlled by the same dominant gene but further evidence is required before this view can be regarded as conclusive. Attempts to utilise the resistance of *S. chacoense* in general breeding have been made by means of the diploid-hexaploid cross *S. chacoense* × *S. demissum* and also by using colchicine-induced tetraploid *S. chacoense* in crosses with *S. tuberosum*. The former approach has been successful and the initial triple hybrids (*S. chacoense* × *S. demissum*) × *S. tuberosum* have been obtained. No success was achieved, however, in the use of tetraploid plants of *S. chacoense* as either male or female parents in crosses with *S. tuberosum*.

A study of the relationships between genes controlling response to virus Y and virus A in *S. demissum* was extended to additional lines of this species and also to an examination of the control of responses to these two viruses in *S. chacoense*, *S. simplicifolium* and *S. stoloniferum*. Parental and $F_1$ material was tested with the two viruses during the year and breeding appropriate to the continuation of the study was carried out.

The genetics of reaction to virus X in *S. acaule* were further explored in an examination of two large $F_3$ progenies after inoculation with the virus strains $X^L$ and $X^B$. It was found that seedlings which were susceptible to and tolerant of $X^L$ were also susceptible to and tolerant of $X^B$. On the other hand, seedlings

which reacted to sap-inoculation with $X^L$ by showing a localised necrosis usually showed no response to $X^B$. Infection of these seedlings by graft-inoculation with $X^B$, however, invariably induced a necrotic response and it is concluded that a single pair of genes controls reaction to both strains of the virus.

Progress was made in the utilisation of the resistance to virus Y found in *S. stoloniferum* and *S. phureja*. Over 3,000 seedlings in the fourth generations from these sources were tested in the greenhouse for resistance to virus Y prior to selection for improved types in the field. Representatives of an earlier generation were tested with four strains of virus Y which differ in their pathogenicities towards cultivated varieties. All the material tested resisted all four strains and thus supported earlier indication that the resistance derived from each species operates against a wide array of Y viruses and not only against specific strains.

In breeding for resistance to leaf-roll, only one seedling, raised in 1949, reached the final infection trial in 1957. This seedling contracted 3 per cent infection in that year as compared with 7 per cent infection in Arran Banner and 19 per cent infection in Dr McIntosh. A further 11 seedlings were entered into this trial in 1958.

Seedling progenies bred from the American variety Saco which is apparently immune to virus S have been examined for their responses to sap-inoculation with this virus but at present it is not possible to say if the immunity has been transferred to any of the derivatives.

Work on virus diseases was extended during the year to include virus diseases of grasses and cereals. In a preliminary study, a search was made for infected plants among the grasses and cereals grown at Pentlandfield and elsewhere. Symptoms of barley yellow dwarf virus, a virus known to occur widely on oats in England, were not seen in any of the oat crops examined. Occasional plants were seen with reddened leaves but these plants were of normal height and when they were colonised with aphids, *Rhopalosiphum padi*, no virus could be transmitted to healthy oat seedlings. Similar tests were made on perennial ryegrass but again no virus was demonstrated. Barley yellow dwarf virus is dependent upon aphids for its spread into cereal crops from the over-wintering sources of infection and, if the virus is present in Scotland, it may infect the cereal crops only in those years when aphids are abundant.

This year very few aphids were seen on the cereal crops examined.

Using *Rhopalosiphum padi*, a virus was transferred from stunted *Festuca ovina* plants to oat seedlings in which it caused severe stunting and leaf malformation. A virus less damaging to oats was found in *F. ovina* plants of normal appearance and may have been present also in the stunted plants although this has not been demonstrated. The identities of these viruses have not been determined. The fact that neither disease was seen in oats growing near the *F. ovina* suggests that no suitable vector migrated from the *F. ovina* to the oats.

Sap inoculation to seedlings of Italian ryegrass demonstrated the presence of ryegrass mosaic virus in plots of perennial ryegrass. The infected plants were mottled but did not appear to be severely damaged. An attempt is being made to estimate the losses caused by this virus. An antiserum to the virus has been prepared which will facilitate testing on a larger scale.

**Brassica Crops.**—The examination of hybrids between thousand-head kale and the horticultural forms heading broccoli, sprouting broccoli, kohl rabi and cabbage has been continued. *Thousand-head kale* × *heading broccoli* : A number of hybrid progenies derived from crosses involving late and early broccoli cultivars are being studied, and two hybrid families of Royal Oak origin are of particular interest. When, however, the early Veitch's Self Protecting broccoli is used as a parent, there is a wide difference in parental maturity types, and earliness predominates in the first two generations. A great deal of selection has been carried out on these hybrids in an attempt to eliminate bolting from an otherwise attractive type with short stem and rosette habit. *Thousand-head* × *kohl-rabi* : The search here, too, has been for resistance to bolting. Hybrids derived from the kohl rabi cultivars " Vienna " and " Prague " have given the best leafage, but are susceptible to bolting. A short stem, with or without short side stems carried a rosette of very numerous leaves, but the yield is too low, except perhaps late in the season. It is doubtful whether the various degrees of bulb formation are of much feeding value, and the unthickened stem, a recessive condition, might be associated with more leafage. *Triple hybrids* of kale, broccoli and kohl rabi, are also being examined for suitable combinations of characters.

Recently attention has shifted to two other hybridisations. *Thousand head* × *sprouting broccoli*: Neither the $F_1$ hybrids grown in 1957 nor some populations of $F_2$-generations growing on a relatively good piece of land in 1958 have held out any promise that good types may emerge from this hybridisation, and work upon it has been discontinued. The stems are long and the leaves have small blades on long petioles. *Thousand-head* × *cabbage*: Here again there is a wide range of maturity types accentuated by the specialised behaviour of spring cabbage varieties. Various crosses have been made, and it was the spring varieties whose flowering most often coincided with the kale. Nevertheless out of 22 populations of $F_1$ plants grown in 1958, nine were of January King parentage and a few were progenies of Large York and Christmas Drumhead. Only one $F_2$-generation was available, and this was from a spring cabbage. Some bolting tendencies were observed.

*Thousand-head kale.*—It is apparent that there is greater uniformity, in respect of some group of characters, in "Canson" and possibly in some other special strains than is found in the general purpose varieties of thousand head. Selections of plants of different appearance have been made and cuttings rooted in the greenhouse have been used for obtaining hybrid and selfed seed. The whole plants, grown together in isolation plots, give open-pollinated seed in quantities sufficient for close sowings. When grown close together side shoots are suppressed and indeed seem unnecessary. At wider spacing plants show a great deal of variation as to when and how fast their side buds develop into shoots. Branching before winter would seem desirable, though too early development may give excess of woody side stems. The type with buds still dormant in winter seems definitely inferior.

The 1958 trials included some progenies of plants with a rosette of narrow, erect leaves and plain margins. There were also a few leafy marrow stem types, originally selected from crosses between plants of a short-stemmed marrow kale × New Zealand hybrid kale. One or two lines seem worth keeping, but the highest yields of leafage are found on types with long stems.

*Swedes.*—The examination of self-sterility occurring in a strain of swede was continued. Hybrids of self-sterile × normal swedes were grown and kept for testing, while second-year plants were bagged during flowering.

A yield trial was laid out with thirteen Station strains of swede and three control varieties. Six strains derived from the cross AOE were all heavy yielders, and three of them gave yields of dry matter at least equal to that of the best control. It was decided that one of these, which had better shaws than the others, should be multiplied and given further tests.

The artificial "swede" obtained by crossing Bruce turnip with a hybrid kale, has been carried on a generation by hand-pollination in self- and sib-matings. It is very self sterile, but crosses readily onto natural swede and rape. There is now sufficient material for cytological and morphological examination.

**Sugar Beet.**—The sugar beet report is for the year which ended on 31st March 1958. A similar programme is in progress for the current year, but the results have not yet been analysed.

Experimental strains and polycross progenies bred by the Plant Breeding Institute, Cambridge, were sown on 29th March in a trial at Musselburgh, Midlothian, and a test of bolting was obtained. The control, Klein AA, had 13.8 per cent of bolters by 25th September, whereas the experimental material ranged from zero to 5.4 per cent.

The Scottish Station material in trial at Musselburgh consisted of inbred- and polycross-samples of Logie families, and bolting ranged from 0.2 to 7.5 per cent, compared with 13.2 per cent in Klein AA and about 20 per cent in the Klein E control.

Another trial of Station material was sown at Pentlandfield, but not until 9th April, when conditions were less conducive to bolting. Indeed most of the lines showed no bolting, though two of them and the Klein E control had about 7 per cent by 19th September. Most of the material being assessed was descended from plants selected at Logie Farm, Newburgh, Fife, in 1948. Bulk samples containing progenies of groups of mother plants were compared at Musselburgh and the offspring of single, open-pollinated mother plants at Pentlandfield. Two families, Logie-5 and -F, had been outstanding in 1956, and though there was no test of the actual lines which were undergoing multiplication at Cambridge, some other lines of these families were examined. Logie-3 and -13/21 were families somewhat intensively selected because of promise shown in early generations, but several lines of each at Pentland-

field yielded poorly, as also did an inbred bulk sample and a polycross of Logie-13/21 at Musselburgh.

Attempts to improve the yield of this non-bolting family have not been successful. Only four polycross samples were available and these had been obtained by seeding plants of four families together in a greenhouse, and harvesting the seed from plants of each family separately. When these polycrosses were compared at Musselburgh with bulk samples of their respective lines, little heterosis was shown. Figures for two of these families are given in Table I.

## TABLE I.

COMPARISON OF POLYCROSS AND LINE-BRED SAMPLES OF TWO FAMILIES OF SUGAR BEET SOWN 29/3/1957 AT MUSSELBURGH.

| Family | Logie-D | | Logie-13/21 | | |
|---|---|---|---|---|---|
| Breeding | Poly-cross | Inbred line | Poly-cross | Inbred line | Signif-icance (P=1%) |
| *Percentage bolted on—* | | | | | |
| 9th July | 0·2 | 0·0 | 0·2 | 0·0 | |
| 1st August | 1·9 | 1·0 | 0·5 | 0·0 | |
| 25th September | 3·1 | 2·9 | 1·0 | 0·5 | |
| *Mean plant value—* | | | | | |
| Top weight, lb. | 1·39 | 1·15 | 1·71 | 1·50 | 0·27 |
| Root weight, lb. | 0·76 | 0·70 | 0·68 | 0·67 | 0·12 |
| Sugar in root, lb. | 0·122 | 0·116 | 0·119 | 0·106 | 0·026 |
| Sugar percentage | 16·1 | 16·6 | 15·6 | 15·6 | 1·0 |
| Noxious nitrogen | 0·45 | 0·42 | 0·60 | 0·52 | 0·18 |

The top weights were heavier in each case, but not significantly. There was some similarity between the performance of polycross and line.

Another late-sown trial at Pentlandfield contained small lots of seed obtained by crossing plants in the greenhouse. The parents of these crosses had been light-treated to obtain resistance to bolting, but sowing was too late to afford an adequate test. The chief purpose of breeding this group was

to find a large shaw type combined with bolting resistance and a good root. Among the twenty progenies in the trial several good shaw types were noted. These were lifted and examined for root weight and shape and specific gravity. All but one were discarded, and plants were selected from this by individual performance. These were subsequently seeded.

The other trials were carried out in connection with a joint investigation into the effects of seed bed and steckling culture on resistance to bolting. The part undertaken by this Station was the growing of sugar beet plants in unthinned seed-beds sown on different dates during the summer, and the testing of progenies, which had been seeded under different conditions at Cambridge. A small yield trial was sown on 2nd April, in which six progenies were compared for bolting, which showed distinct differences according to the treatment. The crop from each plot was later lifted and topped, the tops weighed and the roots sent to Cambridge for analysis. The other trial was in the form of seed beds. Each treatment consisted of four plots, of 10 rows eight inches apart and containing roughly 1,000 clusters. These plots were hand weeded but left unthinned and the bolters were counted and removed at intervals. Two replications were sown on 18th March and the other two on 1st April, and bolting was severe for both dates. Besides providing information as to susceptibility to bolting, one treatment was used as a source of unbolted stecklings for further experiments at Cambridge.

Hybrid monogerm × multigerm plants were backcrossed to multigerm in accordance with a scheme devised by H. Savitsky for the transference of the monogerm character into a desirable strain. Pollen-bearing plants were also tested on annual male-sterile females to ascertain their suitability for breeding male-sterile races. A suitable male parent will give progenies that are all male-sterile, but many beet contain genes that partially restore pollen production in the offspring, which is highly undesirable. Annual male-sterile plants are used for testing to save time.

## Publications

Dunnett, J. M. Variation in pathogenicity of the potato root eelworm (*Heterodera rostochiensis* Woll.). Technique and results of testing wild species for resistance. *Proc. of the Potato root eelworm Symposium, Gross-Lüsewitz*, 1958. (*In press.*)

The eelworm resistance of *S. tuberosum* subsp. *andigena* C.P.C. 1673 is effective against the Boghall population of the potato-root eelworm but breaks down against the Duddingston population. The resistance of *S. famatinae* also broke down against the Duddingston population but to a less extent. The reverse situation held for *S. demissum* and certain unidentified triploid potatoes, which were more susceptible to the Boghall population than to the Duddingston population. *S. vernei* was equally resistant to both populations. There was evidence, therefore, of a complex interaction between resistance types and pathogenicity types.

Several collections of wild potatoes were screened for alternative sources of resistance to the Duddingston population, to replace or supplement the resistance of *S. vernei* if the need should arise. Most of the wild potatoes had some resistance to the Duddingston population. Some seedlings of *S. multidissectum*, *S. neohawkesii*, *S. sanctae-rosae*, *S. megistacrolobum* and *S. raphanifolium* remained free from cysts and were selected for further investigation.

Watson, Patricia J. (1958). The distribution in Britain of diploid and tetraploid races within the *Festuca ovina* group. *New. Phytol.*, **57**, 11-18.

*Festuca ovina* L. is reported to be diploid at least in Scandinavia and in the North Western area of the European continent where a tetraploid is very rare indeed. In Britain, however, a tetraploid race is widespread in Ireland, Wales and the South of Scotland. The diploid occurs only in small pockets of dry sandy heath in the South of the British Isles, is found with the tetraploid in the North of England and South of Scotland whilst in the North beyond the Great Glen it is the sole race.

Suggestions for the origin of the tetraploid are made and it is proposed that there is sufficient evidence to equate the tetraploid with *F. ovina* L., the diploid with *F. tenuifolia* Sibth., although it is difficult to distinguish between the two chromosome races morphologically.

# CULTIVATED *BRASSICEAE*: INFORMATION AVAILABLE TO THE BREEDER

V. McM. Davey

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## I. The Earlier Work

It has been suggested that the Brassicas have received scant attention cytogenetically, but though the lists of articles devoted to these crop plants may compare unfavourably with those of some graminaceous genera, many of the contributions were of first rate importance when published. Three reviews indicate the expansion of the work during the present century : Malinowski (1929) lists 35 references to work with Crucifers ; Hector (1937) gives 80 of which at least 50 relate to cytogenetic aspects, and Yarnell (1956) has a bibliography of 288 items. This last review is most comprehensive ; it summarises all that has been discovered about inheritance in the cultivated forms of Cruciferae, and the results of hybridisation. In some years time it may be necessary to review the subject afresh, but there is no intention of doing so here. Attention will be drawn to some work, mainly recent, which has not been mentioned by Yarnell, and such references will be given at the end, and indicated in the text by the use of capital letters for the author's name. It is desired, however, to refer to much, though by no means all of the literature cited by Yarnell, and rather than publish an incomplete and consequently misleading bibliography, such references will not be detailed here, but the number of the article in Yarnell's list will be quoted against the author's name in small type.

The period reviewed by Malinowski (1929) ended about 1927, and during the first quarter of the century the Mendelian laws of inheritance had been applied to European forms of *Brassica oleracea* L., the 'cabbage tribe,' *B. rapa* L., the turnip, *B. napobrassica* (L) Mill, the swede or rutabaga, and *B. napus* L. the swede-like rape. Sutton (1908 : see Yarnell 231) had striven to apply simple factor differences to segregations in *B. oleracea* some of which were found to be more complex when re-examined by Kristofferson (1924 : Y111, 1927 : Y112), Malinowski (1929 : Y134, the review summarises his earlier papers) and Pease (1926 : Y183, 1927 : Y184). The last two workers established complex linkages with factors of polymeric characters. Allgayer (1928 : Y3) and Pearson (1929 : Y177) also published about this time, and Magruder and Myers (1933 : Y129) and Kwan (1934 : Y118) continued investigations on colour inheritance, otherwise little genetical

work for its own sake has been done with *B. oleracea* since this period. Genetical information has not infrequently been obtained in connection with other work, notably the very extensive pathological and physiological investigations carried out on the cabbage in the United States (*e.g.*, Pound and Walker (1951 : Y190)).

The parallel series of colour and shape characters exhibited by the swede and the turnip have long excited interest. Kajanus (1913 : Y92) first investigated the Mendelian inheritance and formed the opinion that some of the colour characters were unstable ; he later (1917 : Y93) found that dominance was carried into hybrids between the two species. Hallqvist (1915 : Y69, 1916 : Y70) who collaborated in these experiments drew attention to the duplication of factors in the swede. The present writer could find no linkage among the colour characters of the swede (1932 : Y37). Sterling (1951 : Y225) showed that there were at least four genes affecting resistance to clubroot in the swede, and he also found no linkage between these and the colour of the flesh. Flower colour is either strongly linked with colour of flesh, or is controlled by the same factors. Sylven (1927 : Y233) found two factors governing flower colour in the swede-like rape. Recently Shibutani and Okamura (1957) have studied the $F_0$-$F_1$ generations of crosses between turnip varieties and note the behaviour of genes governing characters which they had previously used (1954) for distinguishing between European, American and Asiatic forms of turnip —*e.g.*, the Japanese varieties are generally glabrous (recessive), and the epidermal cells of the testa swell on absorbing water (dominant to non-swelling). It is not proposed to give a more detailed account of the genetics of the Brassicas here ; this aspect is fully dealt with in the three reviews.

Apart from genetics, investigations were only just beginning in 1927. Interspecific hybridisation was confined mainly to crosses such as swede × turnip, which were later to be regarded as the backcrossing of an amphidiploid with one of its parent species, but Sinskaya (1927 : Y221) tested the intercompatibility of most of the species. (See Table I.) She also mapped the distribution of the cultivated forms, and noted differences characteristic of their regions of origin (1928 : Y222). The Russian workers were also to the forefront with intergeneric hybridisation. Karpechenko (1927 : Y103) had pursued his investigations on *Raphanus sativus* L. × *Brassica oleracea* L. to

# TABLE I.

CROSSABILITY OF DIFFERENT SPECIES OF BRASSICA (AFTER SINSKAYA, E. N. (1927 : Y221)). *Bull. Appl. Bot. & Plant-breeding*, **17** : 3-166.

| | | |
|---|---|---|
| *I. Species not crossing with one another* | | |
| 1. *B. nigra* BOCH. | × *B. juncea* CZERN. | |
| 2. ,, ,, | × *B. campestris* L. | |
| 3. ,, ,, | × *B. napus* L. | |
| 4. ,, ,, | × *S. arvensis* L. | |
| 5. ,, ,, | × *S. alba* L. | |
| 6. *Sinapis arvensis* L. | × *B. juncea* CZERN. | Reciprocal matings |
| 7. ,, ,, | × *B. campestris* L. | not carried out in |
| 8. ,, ,, | × *B. napus* L. | Nos. 1-14. |
| 9. ,, ,, | × *B. oleracea* L. | |
| 10. ,, ,, | × *S. alba* L. | |
| 11. *B. juncea* CZERN. | × *S. alba* L. | |
| 12. *B. alboglabra* BAILEY. | × *B campestris* L. | |
| 13. ,, ,, | × *B. napus* L. | |
| 14. ,, ,, | × *B. chinensis* L. | Poorly developed seed. |
| *II. Species crossing with difficulty, less than one good seed per pod* | | |
| 15. *B. juncea* CZERN. | × *B. chinensis* L. | No reciprocal. |
| 16. ,, ,, | × *B. pekinensis* RUPR. | Also reciprocal. |
| 17. ,, ,, | × *B. campestris* L. | ,, ,, |
| *III. Species with medium crossability, half seed viable* | | |
| 18. *B. napus* L. | × *B. chinensis* L. | Also reciprocal. |
| 19. ,, | × *B. pekinensis* RUPR. | No reciprocal. |
| *IV. Species easily crossed, normal seed 70-100 per cent* | | |
| 20. *B. juncea* CZERN. | × *B. napus* L. | No reciprocal. |
| 21. *B. campestris* L. | × *B. pekinenses* RUPR. | Also reciprocal. |
| 22. ,, ,, | × *B. nipposinica* BAILEY. | No reciprocal. |
| 23. ,, ,, | × *B. chinensis* L. | Also reciprocal. |
| 24. *B. chinensis* L. | × *B. nipposinica* BAILEY. | No reciprocal. |
| 25. *B. alboglabra* | × *B. oleracea* L. | ,, ,, |
| 26. *S. alba* L. | × *S.* or *B. dissecta* LAG. | ,, ,, |
| 27. *B. campestris* var. *Sarson* Prain. | × *B. napus* L. | Belong to group I. or II. |

*Note.—Sinapis arvensis* = *B. kaber* ; *S. alba* × *B. hirta.* (See diag. I.)

the description of polyploid derivatives. Otherwise little cytological work had been attempted, and MALINOWSKI's (1929) review gives only a list of chromosome numbers for species, in which *B. napus* is still classed as 2n = 36. Various conditions of self- and cross-compatibility had been described, but no hypothesis had yet been advanced to account for them. Detjen (1926 : Y42) isolated four types of incompatibility in common cabbage, and Stout (1922 : Y226) observed grades of compatibility in *B. chinensis* and *B. pekinensis*. Kakizaki (1922 : Y94) also studied self-sterility in the Chinese cabbage. Hybrid vigour in cabbage was examined by Kotowski (1926 : Y114). Nelson (1927 : Y165) found different degrees of fertility in crosses between forms of the cabbage tribe.

A review of work up to 1937 is given in J. M. HECTOR's 'Introduction to the Botany of Field Crops.' There is little new in genetics but during the ten years 1927-1937 interspecific hybridisation made great strides. Frandsen and Winge (1932 : Y55) found an amphidiploid of swede × turnip, the so-called *B. napocampestris*, which supported the latter's theories on species formation. Catcheside (1934 : Y28) demonstrated chromosome pairing and secondary association in the swede × turnip (*B. napobrassica* × *B. rapa*, and U (1935 : Y257) found a somewhat different picture in the swede-like rape × turnip-like rape *B. napus* × *B. campestris*). The Japanese workers had become very active : Morinaga and others were hybridising within the 10-chromosome species and between members of this large group and species with other chromosome numbers. In 1934 Morinaga (Y153) propounded a genomic hypothesis to account for three elementary species groups and three natural amphidiploids supposedly derived from them (the six groups linked together in Diagram I.). The obstacle preventing European workers from reaching this conclusion had been the supposed chromosome number of *B. napus* and *B. napocampestris*, but U (1935 : Y257), showed that *B. napus* like the similar Eastern form, *B. napella*, had 2n = 38 chromosomes, and he synthesised this amphidiploid from the cross *B. campestris* L. × *B. oleracea* L. Howard (1938 : Y78) confirmed the chromosome number of 2n = 38 for the swede ; previously a pair of very small chromosomes had been regarded as trabants. Intergeneric work had been continued by Karpechenko and others, who crossed the *Raphano-brassica* with various Brassica species. Terasawa (1932 : Y244, 1933 : Y245) obtained a

second amphidiploid called *Brassico-raphanus* from *B. chinensis* (2n = 20) × *Raphanus sativus* (2n = 18).

A great deal of work was done on incompatibility, especially by the breeders of oil-seed forms. The interpretation of incompatibility phenomena in *Nicotiana* had been clarified by East and Mangelsdorf (1925), but this oppositional hypothesis was insufficient to explain the behaviour of Brassicas. Kakizaki (1930 : Y98) postulated sympathetic factors, **T**, as well as the oppositional allelomorphic factors, **S**, to account for the results he obtained with cabbage, and Stout (1931 : Y227) reached a similar conclusion for *B. pekinensis*. Later workers devised other modifications to fit their data, but the principle of gametophytic control was accepted until challenged by Bateman (1954).

There is not a convenient review for the next decade, but 1938-1947 was a period of great activity. The exploitation of colchicine facilitated work on polyploidy. Howard (1939 : Y80, Y81) and others studied autopolyploids. K. J. Frandsen (1943 and 1947 : Y54) set out to synthesise amphidiploids to prove that the natural amphidiploid species had arisen by chromosome doubling of hybrids between the elementary species. Others—*e.g.*, Rudorf (1943), Howard (1942 : Y83) were also making the hybridisations with various objects in view. A great many articles on *Brassica* hybridisations and karyological studies were published in Japanese journals, and these are often known only by title or by short abstracts. Meanwhile, J. C. Walker, who had been publishing since 1926, and his colleagues in the U.S.A. were carrying out intensive pathological and nutritional studies with the cabbage, which frequently led to reports of hereditary resistance, and sometimes to the definition of genes.

## II. Present Information

Yarnell's review, published in 1956, contains a mass of information systematically arranged in a highly compressed form. Attention may be drawn to a table which brings together the taxonomic names, chromosome numbers and common names in English, French and German of all the different forms, and another table listing the genes described for *B. oleracea*. It is evident that the greatest amount of genetical

and phytopathological investigation has centred on the cabbage and other forms of *B. oleracea*, though one may suspect that a Japanese reviewer could greatly amplify the account of the Asiatic vegetables. The results of hybridisation are noted under the parental chromosome numbers and the size of the section devoted to intergeneric hybrids of *Raphanus* and *Brassica* indicates the importance that has been attached to this phenomenon. The articles which have appeared since the period under review have mostly been concerned with the production or fertility of auto- and allopolyploids, the most interesting developments perhaps being the physiological studies of seed development by HÅKANSSON (1956) and the new hypothesis to account for incompatibility which has been developed by BATEMAN (1952, 1954 and 1955). Before discussing these aspects, however, it may be as well to present a brief account of the Brassica forms and their hybridisations.

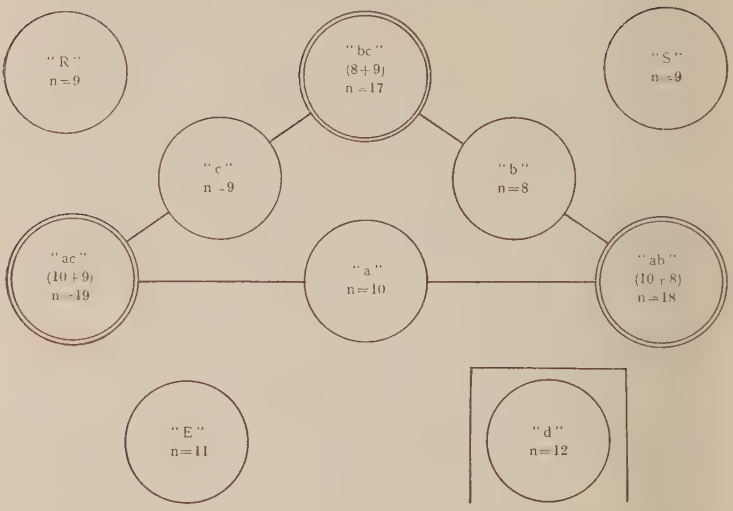
*The genomes.*—If the ability to exchange genes be taken as the criterion of membership to a unit, then this " coenospecies " would contain not only a large number of taxonomic species of *Brassica*, but would also overflow into the genera *Sinapis*, *Raphanus* and *Eruca*. Differences of opinion have existed among cytologists as to the basic number of the *Brassica* ancestor ; Sikka (1940 : Y218) outlined a scheme of evolution based on b = 5 (see Diagram II., page 41), but b = 6 and b = 4 have also been suggested as basic numbers to account for certain cytological findings (Catcheside 1934 : Y28, 1937 : Y29 ; Richharia 1937 : Y201). No forms with less than N = 8 chromosomes are known to exist, and the coenospecies as visualised by breeders hinges on three genomes " a," " b " and " c," with n = 10, 8 and 9 chromosomes respectively (Diagram I.).

The genome " b " (n = 8) has so far proved least versatile, since the cultivated form of *B. nigra* L., the seed of which is used in the manufacture of mustard condiment, differs little from the wild species ; it has attracted attention as a weed after introduction into America.

The genome " c " (n = 9) has given rise to the highly diversified forms of the ' cabbage tribe.' Usually these are regarded as sub-species of only one species, *B. oleracea* L., but the kohlrabi has sometimes been raised to specific rank, *B. caulorapa* Pasq. The wild cabbage *B. oleracea* L., inhabits the coastal regions of the Mediterranean and Western Europe, and there

## DIAGRAM I.

### Genomes of *Brassiceae*




| *Genome* | *Constituents* |
|---|---|
| " a " | *B. campestris* L., including wild sp., oil-seed and fodder turnip-like rapes; Indian oil-seeds, toria and sarson. Oriental vegetable spp., *B. pekinensis* (Lour) Rupr., the Chinese cabbage, *B. chinensis* Jusl., Chinese mustard, *B. japonica* Sieb., curled mustard, etc. (see Yarnell, 1956, page 86). Also wild sp. *B. tournefortii*. |
| " b " | *B. nigra* (L) Koch, wild sp. and black mustard. |
| " c " | *B. oleracea* L. wild sp. and all members of the cabbage tribe; *B. alboglabra* Bailey Chinese kale; Mediterranean island spp. |
| " d " | *B. hirta* Moench (formerly *Sinapis alba* L.) White mustard, not yet successfully hybridised with the others. |
| " E " | *Eruca sativa* Mill. Rocket salad. |
| " R " | *Raphanus sativus* L. Radish. |
| " S " | *B. kaber* (D.C.) L. C. Wheeler (formerly *Sinapis arvensis* L.) charlock, a weed of cultivation. |
| | *Natural amphidiploids* |
| " ab " | *B. juncea* (L.) Coss, brown mustard, Chinese mustard, Leaf mustard. |
| | *B. cernua* Forbes & Hemsl. |
| " ac " | *B. napus* L. Annual and biennial oil seed rapes, colza, fodder rapes, dwarf and giant, Essex, hungry gap kale, etc. |
| | *B. napobrassica* (L.) Mill. (Frequently grouped as *B. napus*.) White- and Yellow-fleshed swede or swedish-turnip Rutabaga. |
| " bc " | *B. carinata* A. Br. Abyssinian mustard. |

are other taxonomic species with the same chromosome number on islands of the Mediterranean, and also a closely related oriental species, *B. alboglabra* (Sinskaya 1928 : Y222).

The genome " a " (n = 10) has a great diversity of forms and a very wide distribution. The wild species, *B. campestris* L. extends from the British Isles to Korea (Sinskaya 1928 : Y222) and is highly compatible with numerous cultivated forms of the same chromosome number. These include phenotypically similar forms of *B. campestris*, the annual and biennial oil-seed rapes and the Indian sarson and toria ; the turnip forms, *B. rapa* L. similar in leaf and flower but with highly specialised storage organs, and finally several Asiatic " species," the Chinese cabbages and mustards, which have been highly developed as vegetables. The most familiar of these are *B. chinensis* Jusl., *B. japonica* Sieb. and *B. pekinensis* Rupr., but others are listed by YARNELL (1956, p. 86). Olsson (1954 : Y175) would reduce all these to sub-species of *B. campestris* on their breeding behaviour, and Sikka (1940 : Y218) regards them as differing only in Mendelian factors. Nevertheless, Olsson found some differences in hybridisations, and he excluded one wild, island species, *B. tournifortii*, which Sikka had included, on the grounds that it was not fully compatible with *B. campestris*. Over such a wide distribution, similar forms could have been domesticated by man in more than one centre, or having been distributed by trade or human migrations, a vegetable form might subsequently become differentiated. The turnips in different parts of the world manifest genetical differences (SHIBUTANI and OKAMURA, 1954).

There are three other genomes which can be hybridised with members of the *Brassica* group. Genome R, with n = 9 chromosomes is represented by the radish, *Raphanus sativus* L. ; genome " S " also with n = 9 chromosomes is found in the weed charlock, *B. kaber* (D.C.) L. C. Wheeler (formerly *Sinapis arvensis*) ; and genome " E " (n = 11) is possessed by the rocket-salad, *Eruca sativa* Mill. Attempts to hybridise white mustard, *Brassica hirta* have hitherto failed ; its chromosome number is n = 12 and YARNELL (1956) has suggested " d " as the designation of this genome.

There are very many hybridisations that have been or could be attempted within and between these six genomes, and there are at least two methods of approach—at the diploid and

tetraploid levels. Either method might be employed to obtain a stable amphidiploid race, but whereas the $F_1$-hybrid of diploid parents requires treatment to double its chromosome content, the $F_1$-offspring of autotetraploids is already in the amphidiploid condition. In the karyological studies of Mizushima (1949) crosses were made at both levels.

Three natural amphidiploids have the genomes "a + b," "a + c" and "b + c" respectively. Genome "bc" (n = 17) is contained in *B. carinata* A.Br., the Abyssinian mustard, and genome "ab" (n = 18) is represented by two species *B. cernua* Forbes and Hemsl. and the polymorphic leaf-mustard, *B. juncea* (L.) Coss. The latter has largely replaced *B. nigra* as a source of mustard condiment, but it has many other uses in Asia where eight major groups of cultivated forms are distinguished (Kumazawa and Abe, 1951, 1955)—viz., one oil-seed, one tuberous-rooted, one tuberous-stemmed and the rest leaf-variants. The third amphidiploid, genome "ac" (n = 19), is of world wide importance. There is no known wild species, but the swede-like rape, *B. napus* L. includes annual and biennial oil-seed forms and fodder forms such as giant and dwarf rape, rape-kale and hungry-gap kale, as well as vegetable, asparagus kale. The root bearing form, the swede or rutabaga, *B. napocampestris* (L) Mill, has the same chromosome number and crosses readily with the swede-like rapes, but the behaviour of the two forms in crosses with 10-chromosome species is not identical (see below). The apparent progression of domestication from the wild plant through annual and then biennial rape and finally to the form with the edible storage organ, may have occurred at both levels but it is also possible, as Yarnell points out, that *B. napocampestris* may not have originated from *B. campestris*, but by the hybridisation of *B. rapa* with some form of *B. oleracea*.

*Hybridisation within the genome.*—Within the genome "c" Sinskaya (1927 : Y221) found that *B. oleracea* crossed readily with an Asiatic species, *B. alboglabra* giving viable seed. Nelson (1927 : Y165) obtained complete fertility in crosses between most forms of the cabbage tribe ; some of the matings gave lower percentages of seed per pod, but this could have been due to chance interactions of compatibility factors. In genome "a" wild species can be crossed (Sikka, 1940 : Y218) and the cultivated species are in general quite compatible, though Yarnell (1956, p. 125) draws attention to a case of

intersterility between Oriental forms found by Kakizaki (1925 : Y95)—possibly the name of one was incorrectly applied. The question of intracompatibility in genome " b " does not arise since there is no diversity of forms. In amphidiploid " ac," Calder (1937 : Y25) found some differences of fertility between two forms of rape crossed with swede, and some of Sutton's (1908 : Y231) results with " Ragged Jack " kale are difficult to understand, otherwise the group is quite intracompatible. The kale to which Sutton referred is probably extinct. In 1942 THOMAS and CRANE classified the *Brassica* crops and the " Ragged Jack " kale they examined had 2N = 18 chromosomes—*i.e.*, it was a kale of the cabbage tribe (see also Crane (1943 : Y32)). Synthetic " ac " polyploids can be crossed with swede and rape.

*Hybridisation between genomes.*—Hybridisation between genomes a × b, a × c and b × c have been successfully accomplished, and the amphidiploids " ab," " ac " and " bc " have all been synthesised. U (1935 : Y257) crossed varieties of *B. oleracea* × *B. campestris* and obtained from about 1,000 pollinated flowers four hybrids with diploid chromosome numbers 19, 28, 29 and 38—*i.e.*, the numbers expected for " ac," " acc," " aac " and " aacc " respectively. Table II. reproduced from MIZUSHIMA (1949) shows hybrids combining the genomes " bc " and " ab " without chromosome doubling, a few bivalents being possible in both. K. J. FRANDSEN (1943) set out to obtain the amphidiploid " ab " from *B. nigra* × *B. campestris*. His matings with diploid plants failed, but he had prepared autotetraploid forms of both parental species, and was able to intercross these to obtain amphidiploid hybrids in the $F_1$ generation. From about 750 flowers pollinated, some on each species, 33 seeds were harvested of which 13 had 36 chromosomes, the amphidiploid number. (These he called *B. pseudojuncea*.) Frandsen (1947 : Y54) completed his investigation by synthesising the amphidiploids " ac " and " bc " again using autotetraploids of the parental species. From 3,000 flowers of 4n *B. campestris* pollinated with 4n *B. oleracea* 65 hybrid plants were obtained, 37 of which had the 2n = 38 chromosome number (*B. pseudonapus*) the others being irregular. From about 800 flowers of 4n *B. nigra* pollinated with 4n *B. oleracea* Frandsen obtained 26 offspring differing distinctly from the parent species and half of these had the amphidiploid chromosome number 34 (*B. pseudocarinata*).

## TABLE II.

MIZUSHIMA, U. KARYO-GENETIC STUDIES OF SPECIES AND GENUS HYBRIDS AS WELL AS THEIR POLYPLOID DERIVATIVES WITHIN THE TRIBUS *BRASSICEAE* IN CRUCIFERAE. *Jap. Journ. Genet.* 24 (1-2) ; 30-33, 1949.
(All in Japanese, but Table I. shows the following data.)

| Genomes and Chromosome number of $F_1$ | IM | Parentage |
|---|---|---|
| 1 bc, 17 | $(o-4)_{II}+(17-9)_I$ | *B. nigra* (b, n=8) × *B. oleracea* (c, n=9) |
| 2 ab, 18 | $(o-3)_{II}+(18-12)_I$ | *B. campestris* (a, n=10) × *B. nigra* |
| 3 bbc, 25 | $8_{II}+9_I$ | *B. carinata* (bc, n=17) × *B. nigra* |
| 4 bcc, 26 | $9_{II}+8_I$ | *B. nigra* × *B. oleracea* (tetraploid) |
| 5 aab, 28 | $10_{II}+8_I$ | *B. juncea* (ab, n=18) × *B. pekinensis* (a, n=10)<br>*B. cernua* (ab, n=18) × *B. campestris* |
| 6 abb, 26 | $8_{II}+10_I$ | *B. juncea* × *B. nigra*<br>*B. cernua* × *B. nigra* |
| 7 aac, 29 | $10_{II}+9_I$ | *B. napus* (ac, n=19) × *B. pekinensis*<br>*B. napus* (ac, n=19) *B. campestris* ac × *B. campestris* |
| 8 acc, 28 | i) $(o-5)_{III}+(9-4)_{II}+(10-5)_I$<br>ii) $(o-6)_{III}+(9-3)_{II}+(10-4)_I$ | *B. napus* × *B. oleracea*<br>*B. pekinensis* × *B. oleracea* (tetraploid) |
| 9 abc, 27 | i) $(o-9)_{II}+(27-9)_I$<br>ii) $(7-10)_{II}+(13-7)_I$ | *B. carinata* × *B. campestris* ac × *B. nigra* |
| 10 bS, 17 | $(1-8)_{II}+(15-1)_I$ | *B. nigra* × *Sinapis arvensis* (S, n=9) |
| 11 cS, 18 | $(o-5)_{II}+(18-8)_I$ | *B. oleracea* × *S. arvensis* |
| 12 aS, 19 | $(o-5)_{II}+(19-9)_I$ | *B. campestris* × *S. arvensis*<br>*B. rapa* (a, n=10) × *S. arvensis* |
| 13 bcS, 26 | $(o-8)_{II}+(26-10)_I$ | *B. carinata* × *S. arvensis* |
| 14 abS, 27 | $(7-10)_{II}+(13-7)_I$ | *B. juncea* × *S. arvensis* |
| 15 AcS, 28 | $(o-2)_{III}+(10-0)_{II}+(6-28)_I$ | *B. napus* × *S. arvensis* |
| 16 aE, 21 | $(o-8)_{II}+(21-5)_I$ | *B. chinensis* (a, n=10) × *Eruca sativa* (E, n=11) |
| 17 aR, 19 | i) $(o-5)_{II}+(19-9)_I$<br>ii) $(o-3)_{II}+(19-13)_I$ | *B. rapa* × *Raphanus sativa* (R, n=9)<br>*R. sativus* × *B. rapa* |
| 18 aRR, 28 | $9_{II}+10_I$ | *R. sativus* × *B. rapa* (tetraploid) |
| 19 SR, 18 | $(o-3)_{II}+(18-12)_I$ | |

Frandsen's main object was to decide the origin of the amphidiploid species in nature, and in the case of *B. pseudojuncea* and *B. pseudonapus* the resemblance to the natural species was so close that they were difficult to tell apart. *B. pseudocarinata* was rather easily distinguished from *B. carinata*, but there was good accordance between the two forms and Frandsen thought that another variety of *B. oleracea* would have given closer results. Syntheses of *B. napus* and *B. napobrassica* have been carried out by several plant breeders with economic objectives, and these will be discussed in a later section.

Mizushima's karyological studies show (Table II.) that the genome " S " of charlock (*B. kaber* or *Sinapis arvensis*) can be hybridised with genomes " b " and " c," and genome " E " found in *Eruca sativa* can be made to cross with genome " a " : this cross was also effected by U *et al.* (1937 : Y261). From a second table it appears that Mizushima synthesised the allopolyploids, bbSS, ccSS, aaSS, aaEE, as well as aaRR and SSRR involving radish. *Raphanus sativus*, with n = 9 chromosomes comprising the genome R, has been employed in very many matings with Brassicas. The cross between radish and cabbage was first made by Sagaret in 1826, and one hundred years later the first amphidiploid, *Raphano-brassica*, was detected by Karpechenko (1927 : Y103). Terasawa (1932 : Y244) obtained the amphidiploid *Brassico-raphanus* by crossing *B. chinensis* and *Raphanus sativus*, and Morris (1936 : Y157) also made this cross.

*Self-fertility of amphidiploids.*—Bateman (1955) whose incompatibility hypothesis will be found in a later section, concludes that since there is sporophytic pollen determination, polyploidy should not be associated with self-fertility (page 62). Dealing with the apparent exception to this rule—that while the diploid species, *oleracea*, *campestris* and *nigra* are self-sterile, their allotetraploid derivatives, *napus*, *juncea* and *carinata* are all self-fertile, he concludes that this self-fertility must be secondary. " Possibly the incompatibility reaction is lost as superfluous in a species which has a new way of maintaining hybridity." Bateman cites the work of Mizushima (1950 : Y141) as showing that the artificially produced allotetraploids in the *Brassiceae* (including *B. carinata* and *B. juncea*) are self-sterile though with good pollen and fertile in crosses with sibs or related species.

*Amphidiploid × diploid matings.*—There are six hybridisations in which the three natural amphidiploid " ab," " ac " and

" bc " might be crossed with one or other of their genomes, and three ways in which the combination " abc " could theoretically be synthesised from them. There is also the possibility that different members of any genome may not behave in the same way when used in a hybridisation, and this seems to be the case in the cross between " ac " × " a." When rape forms of " ac," *B. napus*, are used the $F_1$ hybrid shows at first metaphase ten bivalents and nine univalents—*i.e.*, bivalents equal to the number of chromosomes in the " a " genome. This was found by U (1935 : Y257) who crossed *B. napus* × *B. campestris*, and is seen to apply to two of the crosses made by MIZUSHIMA (see Table II.), who again used *B. campestris* and also *B. pekinensis*. On the other hand, in the cross between swede and turnip, *B. napobrassica* × *B. rapa*, Catcheside (1934 : Y28) found that the hybrids showed irregular chromosome pairing in MI, viz. $(0-3)_{III} + (12-7)_{II} + (0-7)_{I}$. Referring to Table II., a similar irregularity is recorded for the $F_1$ " acc," when *B. napus* has been crossed with *B. oleracea*, but the $F_1$s of " bbc," " aab " and " abb " show the regular pattern. In item No. 4 of this Table " bbc " the *B. oleracea* parent is qualified by Japanese lettering which also occurs against items Nos. 8 and 18, apparently indicating autotetraploidy of one parent in each case. Item No. 8 apparently compares two approaches to the hybrid " acc," (i) " ac " × " c " and (ii) " a " × " cc."

The $F_1$ hybrids discussed above have consisted of one haploid and one diploid genome, but if their chromosomes were doubled by treatment, or if their parents had each been autotetraploid, the constitution would be one genome diploid and one in a tetraploid state. MIZUSHIMA (1949) in a second Table which is not reproduced here, gives five of the six possible combinations of a + b, a + c, and b + c. At IM he found varying numbers of quadrivalents ranging from $(9-0)_{IV}$ in aaaacc, to $(6-1)_{IV}$ in aaaabb ; no trivalents but widely varying numbers of bivalents and univalents ranging from $(10-0)_{I}$ in aacccc to $(2-0)_{I}$ in bbbbcc. The combination aaRRRR, on the other hand, sometimes showed a sexivalent. Mizushima also shows three hexaploids each containing three distinct genomes, at IM these gave :—

| | |
|---|---|
| aabbcc | $(7-0)_{IV}+(12-27)_{II}+(4-0)_{I}$ |
| bbccSS | $(5-0)_{IV}+(16-26)_{II}+(6-0)_{I}$ |
| aaccSS | $(0-2)_{VI}+(7-1)_{IV}+(14-26)_{II}+(0-4)_{I}$ |

The " abc " amphidiploid could form some quadrivalents, but one of the combinations involving " S," the genome of charlock, has one or two sexivalents. Iwasa (1951 : Y86) studied artificial triploids and hexaploids having the genomes " abc," and Nishiyama (1952) examined the fertility of autotriploids obtained by direct and reciprocal 2x × 4x crosses within the " a," " c," " S " and " R " genomes.

The synthesis of " hexaploid " plants containing three 2n-genomes or one 4n and one 2n-genome does not appear to have met with any economic success so far. Much of the hybridisation of genomes " a " × " ac " was carried out before the nature of the cross was recognised (Wilson 1911, Kajanus 1913 : Y92, 1917 : Y93 and others). H. F. Frandsen's original discovery of the allopolyploid prototype *B. napocampestris* (Frandsen and Winge, 1932 : Y55) occurred during hybridisation work with swedes and turnips. The cross is relatively easy to effect ; the hybrids set some seed in bag isolation and self-fertile lines of monstrous appearance can be developed. The writer (Davey, 1939 : Y38) obtained strains which were almost swede-like by selection and self-fertilisation from the $F_1$ swede × turnip backcrossed by swede. Unfortunately, it was not possible to follow the cytology after the first two generations but some turnip characters were thought to persist, and it is possible that gene exchanges can occur as is sometimes claimed by seedsmen.

A peculiarity of the swede × turnip hybrid, especially in the first two generations, is high susceptibility to monstrous outgrowths. The bulb is often covered with swellings, and the side roots are chains of " hybrid nodules." These are not manifestations of clubroot (*Plasmodiophora brassicae* Woron.) which they resemble, and the cause has perhaps never been fully established. Fruwirth (1922) quoted some investigations by Dr Pekoe which pointed to *Bacterium tumifaciens*, but Bartlett (1928) examined the small nodules which sometimes occur near the uppermost rootlets of the swede and which he regarded as analogous to those on the hybrid, and suggested *Olphidium radicicolum* as the causal organism.

*Haploidy*.—Two reasons for seeking and studying haploids are that they may be converted to homozygous diploids for breeding purposes and that their behaviour in meiosis may afford information as to whether pairing and secondary association found in the more complex genotypes are inter-

or intra-genomic. Haploid mutants of Japanese rape were described by Morinaga and Fukushima (1933 : Y155), and Olsson and Hagberg (1955) collected seven from crops of European rape, *B. napus*. These amphihaploids were expected to contain genomes " ac," 10 + 9 chromosomes, and bivalents ranging from 2 to 9 with modal number 6 were found at meiosis. This was similar to the behaviour of the $F_1$-hybrid of *B. campestris* × *B. oleracea*. Olsson and Hagberg considered that pairing in their amphihaploid rape plants was due to partial homology two-by-two between practically all the chromosomes in the genomes of cabbage and turnip-rape. Absence of autosyndetic pairing in the *campestris* genome was inferred from the work of Ramanujam (1941) who did, however, observe a loosely-paired bivalent occasionally in cells of haploid *toria*. Absence of pairing within the *oleracea* genome had also been suggested by the behaviour of an $F_1$-hybrid " cS," of charlock × cabbage made by U *et al.* (1937 : Y261). In the following year, however, Thompson (1956) found bivalents in genome " c " of marrow stem kale, another form of *B. oleracea*. He studied 54 cells at IM of two haploids and found 38 had monovalents only, 12 had one bivalent and four had two bivalents. Another amphihaploid *B. juncea*, genome " ab " was examined by Ramanujam and Srinivasachar (1943) who found that pairing in this case was very much less than that in the $F_1$-hybrid *B. campestris* × *B. nigra*, with which it should have corresponded. If reference is made to Table I., however, it will be seen that Mizushima found only 0-3 bivalents in a cross of these species. Haploid plants of *B. carinata* were studied by Kuriyama and Watanbe (1950) but no English summary of this work is available. The occurrence of allo- and autosyndetic pairing is also inferred from more complicated matings. Shibata (1956b) crossed 4n-*B. pekinensis* × *B. napus* giving an $F_1$ " aaac," and he found one case of autosyndesis within the " c " genome and 5-7 of allosyndetic pairing between " a " and " c " genomes. To a layman these findings are confusing, but it does look as though the time is approaching when cytologists will be able to present a coherent picture of the mechanisms at work in the group : in particular some clarification of the basic numbers would be welcome.

*Origins of the Brassicas.*—Studies of the morphology and behaviour of the chromosomes mainly date back to the 'thirties. Catcheside (1934 : Y28) made detailed studies of the turnip

and swede and their hybrid. In turnip, *B. rapa* he found 10 bivalents at meiosis and secondary associations not exceeding four in number. He considered the turnip to be a secondarily balanced polyploid but probably with structural change of certain chromosomes superimposed. Richharia (1937 : Y202) examined the cytology of three 10-chromosome species, *B. chinensis*, *B. rapa* and *B. pekinensis*. He points out that " on the basis of somatic chromosomes six principal types, more or less, can be distinguished. But when the secondary associations are considered (the maximum number of associations representing the primary types) conclusions are different —*e.g.*, in *B. chinensis* and *B. rapa* the maximum number of associations observed, six, would give four as the primary basic number, while *B. pekinensis* with five associations would have 5 as basic number." Association between morphologically different types (large and short) was frequently observed which strongly suggested some sort of chromosome rearrangements, besides reduplication. " This makes it difficult to arrive at any definite conclusion with respect to the primary basic number." Richharia indicated the six morphological types of chromosomes by the letters A-F. The haploid formula for *B. chinensis* and *B. pekinensis* was ABCDDEEFFF but for *B. rapa* it was ABCDDEEEFF, only two Fs and three Es instead of *vice versa*. Richharia does not stress this difference and he says that in classifying E and F types an exact line of demarcation is difficult. In the $F_1$-hybrids of *B. chinensis* × *B. pekinensis* and of *B. rapa* × *B. chinensis* pairing was regular at diakinensis, but occasionally two univalents were observed in *B. pekinensis* × *B. rapa*. The above details are mentioned because of the suspicion that *B. rapa* may differ significantly from other members of the genome, but there were no signs here of an abrupt rift between turnip and bulbless forms, or between East and West ; but rather a transition with *B. chinensis* holding an intermediate position. The oriental forms were obtained from Japan, but the seed of *B. rapa* came from " local " seedsmen, which probably means in England, since Richharia had been working at Cambridge, though the paper was submitted from India.

Richharia (1937 : Y201) also studied *B. oleracea*, *Raphanus sativus* and their hybrids. In *B. oleracea* he distinguished morphologically six or seven types of somatic chromosomes (in brussels sprouts). At diakinensis 9 bivalents occurred

regularly in brussels sprouts and curly kale, but a ring of 4 chromosomes was found in cabbage. At first metaphase in curly kale there was secondary pairing, the maximum number of associations being five. In the same year Catcheside (Y29) found only three secondary associations in *B. oleracea*, and gave six as the basic number. Thompson (1950) considered that the two bivalents he found in haploid plants of kale (*B. oleracea*) tended to confirm Catcheside's findings. Haga (1938 : Y68) studied secondary association in relation to the genomes. He considered that a certain amount of homology existed between the different genomes due to their being derived by secondary balance from the ancestral genome of six chromosomes, and his scheme was as follows :—

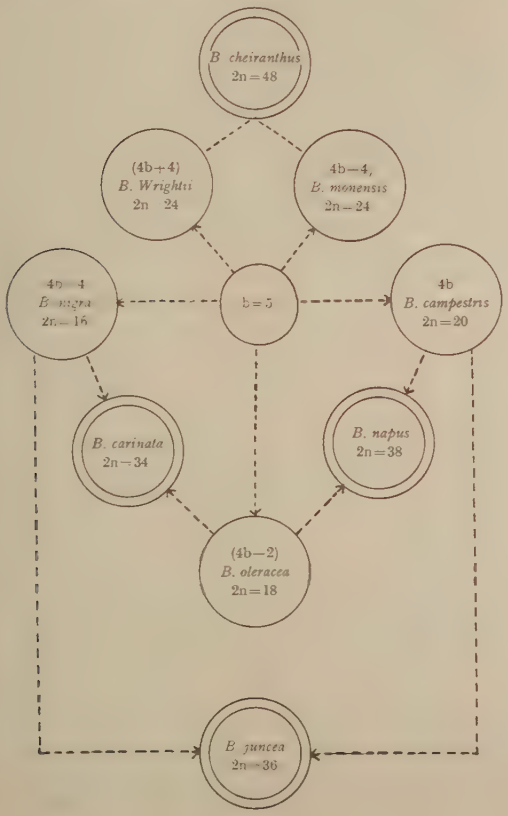
| | | |
|---|---|---|
| Genome "a" | *B. rapa* | AABBCCDDEF |
| "c" | *B. oleracea* | AABBCCDEF |
| "b" | *B. nigra* | ABCDEEFF |

Sikka (1940 : Y218) concluded from an intensive study of three species and from comparison of the secondary chromosome numbers of *Brassica* with the numbers found in related genera of *Cruciferae*, that the basic number of the genus was five (Diagram II.). While some allied genera of *Crucifera* retained the number five as a basis for polyploidy and others later used thirty as a basis for still higher multiples, the *Brassiceae* developed a wide range of secondarily balanced numbers by intercrossing. Of the nineteen species of *Brassica* of which chromosome numbers are known, seven show twenty as the diploid number, three have 2n = 18, two 2n = 24, only one has 2n = 16 and the remaining six have been shown to be amphidiploid derivatives of these. Nearly half the species in the genus have retained the tetraploid number (4b) on the basis of five. The other few with slightly higher or lower number must have resulted by reduplication or loss of certain chromosomes from the 4b number. Thus while some genera of *Cruciferae* related to *Brassica* developed hexaploidy, this genus has developed tetraploidy. Elsewhere Sikka points out that the genus contains seven species having the same chromosome number (2n = 20) but exhibiting wide variations in the morphological characters of the plant. Most of these species cross with each other freely, producing fertile hybrids, some of which have been found to obey Mendelian laws of segregation, and Sikka regards the differences between these species

as due to simple mutations. On the other hand, Brassica includes species with (2n) chromosome numbers of 16, 18, 20, 22, 24, 36, 38 and 48, so that the genus belongs to the allopolyploid class.

## DIAGRAM II.

BRASSICA SPECIES DERIVED FROM A PRIMARY BASIC CHROMOSOME NUMBER OF FIVE. FROM "CYTOGENETICS OF *BRASSICA* HYBRIDS AND SPECIES," BY S. M. SIKKA, *J. Genet.* **40**, page 494.



Sikka's conclusions give the breeder a feeling of optimism about hybridisation within genome " a," whereas Richharia's work, quoted above, suggests difficulties, with possibilities of diminished fertility. Numerous workers have intercrossed 2n = 20 chromosome forms. Olsson (1954 : Y175) having separated the wild *B. tournefortii* Gouan. as a distinct species, reduced most of the cultivated species and forms to sub-species of *B. campestris* L.s.lat. He noted that yellow-seeded sarson is self-fertile and differs from the rest in certain other respects and he had not had the opportunity of placing brown-seeded sarson and *B. parachinensis* Bailey. Beyond listing them as separate sub-species, Olsson makes no distinction between turnip and turnip rape. Sun (1944, 1946 : Y229) made a classification in which he recognised *B. campestris* and *B. chinensis* and suggested that the Brassica species with n = 10 chromosomes had originated in two geographical centres, the Western and the Oriental. Sinskaya (1927 : Y221) considered that *B. campestris* and *B. chinensis* were distinct species or linneons, because certain characters distinguished all the members of each, and because of heterosis in the $F_1$, transgression of vegetative period in $F_2$, and sterility of part of $F_2$.

Wild *B. campestris* is distributed round the world from Ireland to Korea (Sinskaya, 1928 : Y222) and wild *B. oleracea*, or similar 2n = 18 species, occupies the Mediterranean and West European seaboards, and is also found in Eastern Asia (*B. alboglabra* Bailey). Olsson (1954 : Y174) has examined the Japanese cultivated rape form (n = 19), said to have reached Japan from Korea. In crosses with Scandinavian varieties, he found full compatibility and a heterosis in certain characters, and there was nothing to suggest that it is not a form of *B. napus*. The Japanese had called this rape *B. napella* because it had n = 19 chromosomes at a time when European *B. napus* was thought to have n = 18. Olsson points out that *B. napella* Chaix has been used to denote turnip-rape, and is thus a cause of confusion. Regarding the origin of the Japanese form Olsson considers that the natural amphidiploidy could have occurred in various parts of the world where genomes " a " and " c " were both present. Mitsukuri (1956) suggests that the caryotype of Japanese varieties of *B. napus* indicates hybrid origin from *B. oleracea* × *B. chinensis* ; the chromosomes are larger than those of European varieties.

It is very easy to suppose that highly specialised forms of

the genome " a," such as the various Asiatic vegetables and the Indian sarson and toria, have been developed by man in different parts of the world, and it seems probable that the comparatively unspecialised rape forms could have been domesticated from wild populations many times and in many places. If the turnip is a natural development in the selection of rape it also might have more than one source of origin. On the other hand, turnips could have been carried as roots or seed in migrations or along trade routes. The work of SHIBUTANI *et al.* (1952, 1954, 1957) seems to be directed towards assessing the differences between turnips from Japan, Europe and America.

Granted that the turnip and forms of *B. oleracea* have spread over the world, the origin of the swede by hybridisation and amphidiploidy might occur anywhere and on more than one occasion. When they first attained importance in European agriculture, after 1773 in Britain, swedes were of the white-fleshed type, to which the name *napobrassica* is more properly given. They were somewhat fang-rooted, and perhaps more akin to rape than the yellow-fleshed forms, sometimes called *rutabaga*, which later almost entirely displaced them. The " bulb " of the yellow-fleshed swede is more shapely and nearer the turnip in appearance, and in crosses of white × yellow it is very difficult to select lines free from fanginess. The two forms might well have had different origins.

It is usually said that the cultivated forms of the cabbage tribe are all one species, but the assumption that they have a common ancestry is challenged by Ruggles Gates (1953 : Y73) who believes that the vegetable forms were developed in different parts of Europe from the indigenous wild species.

*Autopolyploidy*.—Work on the nature and potentialities of autopolyploids was in progress before the introduction of colchicine. FUKUSHIMA (1931) described chromosome doubling in *Brassica* and how it occurs. Shchavinskaya (1937 : Y213) devised a method which was 27 per cent successful in inducing tetraploidy by removing axillary buds. Karpechenko (1937 : Y106) found that tetraploid cabbage had much greater cross-ability with other species, though not with radish, than had the corresponding diploid. He attributed this to the different segregation of sterility factors and not to the genome ratio. Studies on compatibility in *B. pekinensis* are being carried on by SHIBATA (1955, 1956a, 1957a). In the first paper he gives

the compatibility of tetraploid combinations of known S factors, and this agrees with the expectation for oppositional factors. The third is concerned with reversion to diploidy in a selfed strain of autotetraploid ($S_1S_1S_1S_1$); pollen fertility of the reverted diploid ($S_1S_1$) was 88.9 per cent in contrast with 84.7 per cent in the tetraploid and 96.4 per cent in the original diploid. Kadota and Ito (1952) made attempts to improve fertility and inactivate self-incompatibility in the progenies of autotetraploid *B. pekinensis* and obtained an improved seed set following self-pollination. Bishop (1947 : Y15) has attempted to give a genetical basis of sterility in tetraploid Broccoli.

With regard to the benefits conferred by autotetraploidy Barr and Newcomer (1943) analysed heads of equivalent size of diploid and tetraploid cabbage, about 30 each in one experiment, and found 36 per cent more sugar, 33 per cent more colloidal nitrogen, but 14 per cent less soluble nitrogen in the tetraploid. Moreover the lower leaves of immature tetraploids contained 300 per cent more ascorbic acid than those of diploids. All these percentages are calculated on fresh weight. Tandon (1952) compared a $C_6$ generation of autotetraploid sarson (genome " a ") with a corresponding diploid population and found that the tetraploid had a number of gigas features and was later in flowering. The seed yield was considerably reduced, but this was offset by greater seed weight. An interesting observation was that the tetraploid included 0.7 per cent of natural hybrids with *B. juncea* (" ab ") and no such hybrids were detected among the diploids. Both diploid and tetraploid showed similar degrees of natural crossing with toria (another Indian genome " a " species).

*Endosperm and seed development.*—Ramanujam (1940) found two triploids in cultures of toria and these were bigger than the diploids ; the P.M.C. showed varying numbers of trivalents. In general triploid seed is small and badly equipped for survival ; Nishiyama (1957) was able to sieve triploid seed out of the larger tetraploid radish seed. At meiosis there were trivalents, bivalents and univalents but the number of good pollen grains was unexpectedly high.

Two investigations on seed development are largely concerned with polyploidy though they have wider bearings. Howard (1939 : Y81) found that the tetraploid seed of *B. oleracea* was somewhat heavier than the diploid seed, but that the triploid

seed from the cross tetraploid ♀ × diploid ♂ was very small by comparison, which he attributed to an abnormal endosperm : embryo relationship. He also studied the occurrence of triploids in diploid self- or cross-matings, and also seeds with double embryos. HÅKANSSON (1956) studied normal seed development in *B. rapa* and *B. oleracea*, in the diploid × tetraploid and tetraploid × diploid matings of each, and in the reciprocal interspecific hybridisations. He describes the physiological disturbances occurring in the endosperm development and the probable causes of embryo lethality. Thus the chances are strongly against formation of viable seed both in triploid and hybrid zygotes, and such seed may have to be cultured on special media to survive. SHIBATA (1957b) made reciprocal 4x × 2x crossings of *B. pekinensis* using plants of known genotype, and he found that the percentage capsule set was much higher in compatible crosses (with no *S.* alleles common to both parents) than in incompatible matings. The degree of fertility is not indicated in the abstract. Breeding work is further complicated by ' fruitfulness ' (Nelson 1927 : Y165), where pod development may conceal a complete absence of viable seeds, and also by pseudogamy, where the seeds may prove to be maternal hybrids which frequently occur in interspecific hybridisations (*e.g.*, Mohammad and Sikka, 1940 : Y144).

*Self- and cross-compatibility.*—Various degrees of self-fertility and self-incompatibility are found among the cultivated forms of *Brassica*. The swede sets seed plentifully when the flowering head is enclosed in a pollen-proof bag ; so also do black and white mustards, kohl-rabi and purple sprouting broccoli, while some cabbages, savoys and borecole set no seed under these conditions (Nelson 1927 : Y165). Nelson also showed that the relative maturity of pollen and stigmas may affect the seed set, and indeed it is a general practice to bud-pollinate when attempting to get selfed seed in difficult cases (Attia 1950 : Y5 ; Kakizaki and Kasai, 1933 : Y99 ; TATEBE 1936). Stout (1922 : Y226) was one of the first to describe different grades of self-compatibility in *B. sienensis* and *B. pekinensis*.

Self-incompatibility is associated with degrees of cross-incompatibility, especially in closely related plants. In his " Introduction to the Botany of Field Crops," HECTOR (1936) summarises the complicated findings of the earlier workers,

and shows how an interpretation of these phenomena based on the work of East and Park (1917) and on the genetical analysis of the situation advanced by East and Mangelsdorf (1925) was applied by *Brassica* breeders. The oppositional hypothesis in itself was not sufficient and Kakizaki (1930 : Y98) working on cabbage, postulated sympathetic factors as well, while Stout (1931 : Y227) gave a similar explanation for *B. pekinensis*. Although later workers devised modifications to meet the needs of their data, the gametophytic basis was always accepted.

*Sporophytic hypothesis.*—Bateman (1952) postulated various theoretical incompatibility systems. He noted that different mechanisms had been invoked by earlier authors to explain the results they obtained in three species of *Crucifer*, whereas experience in other plant families had indicated uniformity in the self-incompatibility system operating in a given family. Bateman (1954) then demonstrated " that self-incompatibility in *Iberis amara* is determined by a multiple-allelic system with sporophytic determination of both style and pollen, and independance, dominance and mutual weakening." Bateman's (1955) third step was to examine published data on incompatibility in *Cruciferae*, in *Cardamine pratensis* by Correns, in *Capsella grandiflora* by Riley and in *B. oleracea* by Kakizaki (1930 : Y98). He also analysed his own unpublished data on *Raphanus sativus* and *B. campestris* and found that all these could be shown to be in accordance with the *Iberis* results. The plants of *Iberis* were too short lived to be used for crossing with offspring, but this part of Bateman's hypothesis, together with the general application, was confirmed by Thompson (1957) using the marrow-stem kale form of *B. oleracea* and propagating the key plants vegetatively. Thompson and Howard (1958) have made a further contribution to this subject, which is still in press. Sampson (1957) also found confirmation with 'Calabrise green sprouting' broccoli, and he too analysed some of the data of earlier workers on *B. oleracea*. Four genetic schemes had been proposed to account for observations on self- and cross-incompatibility : " (1) oppositional **S** alleles at one locus, with the pollen behaviour determined gametophytically by the genotype of the pollen itself (Odland and Noll, 1950 : Y171) ; (2) system (1) modified by sympathetic **T** alleles at a second locus to account for instances of self-compatibility (Kakizaki, 1930 : Y98) ; (3) system (1) modified by . . . a

polygenic system (Attia and Munger, 1950 : Y6 ; and (4) a system with oppositional alleles at two loci, with gametophytic control of pollen behaviour (Sears, 1937 : Y212 ; Mizushima and Katsuo, 1953 : Y143)." Sampson considered that the data obtained by most of these workers could be equally well explained by a sporophytic system, but, unlike Bateman, he found that some of the work of Kakizaki provided clear-cut though limited evidence for a gametophytic system which was irreconcilable with the *Iberis* scheme unless contamination be invoked. Thompson (1957) points out that Kakizaki's results are inconclusive owing to the number of seeds per fruit set by compatible pollinations not being sharply distinguished in the plants he studied.

The question of the alternative systems is, of course, much wider than the Brassicas. Brewbaker (1957) has studied the types of pollen in natural orders and has suggested that *binucleate* pollen is associated with stylar inhibition and the gametophytic type of self-incompatibility, while *trinucleate* pollen is correlated with stigmatic inhibition and the sporophytic type, but there are exceptions.

## III. Application to Breeding

Most plant breeding work is limited to some very small corner of the group. Once a variety is in existence and if a constant uniformity of type is desired, it is maintained by commercial seed growers who are constantly selecting within a strain and propagating from a few phenotypically similar plants. In the breeding of a new variety all the sources usually lie within the same form or sub-species, and this is generally the case also in those types of strains that are bred for heterosis. For example, the several families intercrossed to give swede seed are at least all swedes, probably they are all of similar maturity type and possibly even of similar colour and shape. Going rather further afield, the plant breeder may intercross forms of the same species, *e.g.* members of the cabbage tribe, or of the same genome as in the case of hybridisation between 10-chromosome species. The chances of obtaining valuable combinations are possibly more remote, and when they have been identified considerable selection may be needed to bring the hybrid strain up to economic level. Operations of this

sort are being carried out by Institutes and breeders who are able to follow a long-term policy, and so also are operations involving polyploidy and species hybridisation, which require cytological surveillance. The first fruits of the last mentioned operations are now coming into cultivation as autotetraploid and amphidiploid strains, which will now be discussed.

*Autotetraploidy in strain breeding.*—K. J. Frandsen (1945) in a general discussion of polyploidy says " Regarding the tetraploids of the species in which from a practical point of view the fertility is a decisive character (*Sinapis alba* and *B. nigra*) the results of the field trials are not encouraging. The seed yield of 4n *S. alba* amounts to about 50 per cent of the normal yield of the diploid form. The seed production of 4n *B. nigra* is about 60-70 per cent of the diploid form." Frandsen also observes that as a rule tetraploid forms have a longer period of development than diploids. In some species the tetraploid forms appear to be more balanced than in others ; thus the development of 4n *B. nigra* is more harmonious than that of 4n *B. campestris*.

Parthasarathy and Rajan (1953) working with *B. campestris* (toria), experienced difficulty in increasing the fertility of the autotetraploids. After repeated selection among progenies of single plants selected for their high fertility, they changed their method, at the $C_8$ generation, mixed the seed of several superior individuals and isolated the mixture from pollen of inferior sorts. By this means they raised fertility in a further two generations to the diploid level, and they attribute this to greater diversity of incompatibility factors in the plants in the proximity of the mother plant.

Autotetraploid strains in cultivation or nearly ready for the market, include turnips in Sweden and Holland, radish and possibly Chinese cabbage in Japan.

Svalöf's tetraploid Sirius turnip was first marketed in 1953. Josefsson (1955) describes the aims and breeding, from about 1940 when Dr Albert Levan commenced chromosome doubling experiments to 1946 when tetraploid and diploid strains were compared in yield trials for the first time. Tetraploid strains of Bortfelder, Yellow tankard and Östersundom turnips were then intercrossed and those combining to give the best yields were used for breeding " Sirius." By breeding within one variety, tetraploids similar in type and colour to the diploids can be obtained, but the objective was the maximum of

heterozygosity, for which the tetraploid constitution is particularly suitable, so that the ' bulbs ' of Sirius, though medium-long, big and well-formed had very variable skin and flesh colour. The very great root weight, despite relatively low dry matter percentage, gave considerable increase in yield of dry matter over control strains, and further trial results presented in a recent report (Josefsson, 1958) show that this superiority has been maintained. Thousand-seed weight of the tetraploid was 3.8 g. compared with 2.4 g. for diploids, but the yield of seed had not been assessed in 1955.

From information supplied by Dr M. J. Zijp of the " Centraal Bureau," it appears that there are three autotetraploid turnip strains competing for certification in the Dutch Government Trials, these are named :—

Tetraploide Halflange Blauwkop CB,
" " Breedblad CB, and
" Knolvoetresistente Breedblad CB.

The achievements of Japanese breeders were summarised at the International Genetics Symposium, held in Tokyo and Kyoto, by Tanaka (1956) (page 80) and amplified by Yamashita and other breeders (ibid. page 344). The tetraploid radish, " Mino-tetra-Daikon " was produced by colchicine from a Japanese early race called " Minowase." More than a decade has passed since its appearance and its characteristics had been made clear. The tetraploid radish is quicker in growth than the original diploid, it attains a heavier weight and bigger size, it is more resistant to cold, free of hollow heart and late in bolting. Non-pithiness and a good taste are also claimed. The area under cultivation was about 100 ha. in Japan and it was also finding new territory in Hawaii.

*Synthetic amphidiploid breeding.*—Rudorf (1943) produced forms of synthetic rape using 4n *B. oleracea* and 4n *B. campestris* as parents ; his object then was to breed for frost hardiness. He described (1951) his amphidiploid race and crosses between synthetic and natural rape and has recently shown (1958), that the latter are able to outyield commercial rape for seed production and oil content. One of the methods he employed for the production of semi-synthetic amphidiploids was the fertilisation of unreduced egg-cells in the diploid hybrid by pollen of natural rape. The Japanese have certainly marketed an amphidiploid variety derived from *B. pekinensis*

× *B. oleracea*, and known by the symbol "COO" or "CO." It is late maturing and resistant to cold, giving fodder over a long period, whereas the natural rapes are oil plants. "COO" is sometimes used as a vegetable in spring, and about 1,200 acres were under cultivation (YAMASHITA *et al.* 1956).

HOSODA (1952) discusses three different types of artificial amphidiploid *B. napus*—viz., forage types (O) which proved highly cross- and self-compatible; vegetable types (C) which were bad in both respects, and oil types (N) which were somewhat inferior to the "O" types. HOFFMAN and PETERS (1958) discuss seven ways in which attempts were made to produce synthetic and semi-synthetic forms of rape.

Most of the subspecies of *B. oleracea* have been used to produce artificial *B. napus*, but rape-like forms of *B. campestris* have generally been used as parents. Although earlier attempts to use the turnip, *B. rapa*, by Calder (1937 : Y25) and BECKER (1951), had failed to produce $F_1$ plants, OLSSON, JOSEFSSON *et al.* (1955) attempted this cross using several types of turnip, all autotetraploid, and various members of the cabbage tribe as males. They pollinated about 7,500 flowers and obtained 1,619 seeds, but only seven offspring plants deviated from the maternal types, and of these two were quite like the paternal parent; the other five were true amphidiploids. Three of the swede-like hybrids produced families which were intra- and inter-fertile and compatible with true swedes, while the other two were partially cross-sterile. A second batch of 6,400 pollinated flowers yielded two or three true amphidiploids and another six which had not then been identified. One hybrid seed per 1,000 flowers seems to be a likely expectation. It is clear from information obtained from Svalöf that considerable work has been done with the descendants of these synthetic amphidiploids, and that their yielding capacities, both as lines and in combination with true swedes is being assessed in yield trials the results of which are as yet unpublished.

*Uses of haploidy and triploidy.*—It might be desirable for breeding purposes to construct a homozygous diploid by doubling the chromosomes of a suitable haploid. There are various ways of detecting haploids; OLSSON and HAGBERG (1955) selected them from fields of flowering rape by small size of flower, and this characterised the haploid *toria* (RAMANUJAM, 1941), which was also diminutive in plant size. THOMPSON

(1956) made use of a gene causing hairiness in the first leaf of the seedling marrow-stem kale. He crossed recessive females with pollen of a homozygous dominant, and found a few recessives in the offspring. The high infertility of tetraploid × diploid and reciprocal matings (Howard 1939 : Y81, HÅKANSSON, 1956) rules out the use of triploids for the production of "hybrid seed" as has been done successfully in sugar- and fodder-beet breeding.

*Breeding within the genome.*—It is widely believed that new forms of value to man may yet be obtained from the *Brassicas*, and particularly from *B. oleracea*. One way might be from the intercrossing of cultivated forms, or species, of the same chromosome number, and another by extracting something fresh from a wild species. The hybridisation of forms of the cabbage tribe has long been a tempting pursuit, and Mendelian studies have not been conducted without some hope of finding a rare segregate of economic worth (*e.g.*, Pease 1926 : Y183) ; but much disappointment has resulted, though one or two successes have been claimed (*e.g.*, the "caulicab" by Van Clute 1952 : Y263). The polymeric linkages which ensure that characters such as "hearting" and "curled" leaves (Pease 1927 : Y184) do not develop fully on the same plant, have dashed many hopes of obtaining dual-purpose vegetables. Recently the attention of agriculturists has been drawn to the possibilities of devising a much more comprehensive range of leaf-bearing forms. The provision of fresh fodder over a greater part of the year is one objective, and the production of types to meet the requirements of new farming techniques another. At present, setting aside particular uses of cabbage, the chief leaf-bearing crops in Britain are forms of kale, *B. oleracea acephala*, and rape, *B. napus*, while the leaves of turnip and certain forms of turnip-like rape *B. campestris*, can also be fed to stock.

Horticultural forms of the cabbage tribe might contribute useful characters in hybridisations with kales. For instance, if low growth was desired, a recessive gene could be introduced from the kohl rabi. The length of the vegetative phase, or the ability of a form to produce its peak of leafage at a certain time of year, might be attained by crossing kale with suitable strains of forms like cauliflower and heading-broccoli which have a complete range of vegetative phases lasting from a few weeks to over a year. In genome "ac" the choice of hybridisa-

tions is less extensive, but in genome " a " there is theoretically a wide choice of matings, though hidden obstacles such as incomplete pairing of chromosomes might cause reduction of vigour or even abnormality.

Another method of obtaining new forms might be the examination of wild material collected from different regions and grown under good cultural conditions. Ruggles Gates (1953 : Y63) was much impressed by the enormously increased vigour of wild cabbage plants growing in a botanical garden, in comparison with their parents on the cliffs of Dover. He also drew attention to the several supposed countries of origin of the cultivated forms of *B. oleracea* and suggested that untapped sources of variation may be awaiting exploitation.

*Strain improvement and maintenance.*—The work discussed so far may be relevant to the planning or breeding of a new strain, but little has been said about methods of bringing that strain up to economic efficiency or maintaining it at that level. Brassicas have to be regarded as cross-fertilising crops ; this may be obligatory, due to a preponderance of self-sterility, or it may be a balance struck between the activities of insect pollinators and natural self-fertility, as in the swede and swede-like rape. In rape two-thirds of the seed set is selfed (Olsson and Persson, 1958), and the proportion in swede is certainly large. Self-fertility leads towards uniformity of type, but where heterosis is sought it is a disadvantage.

K. J. Frandsen (1952) discussing theoretical aspects, points out that the breeding systems for cross-fertilising plants have developed from simple mass-selection, through systems more or less like those applied for self-fertilising plants, to systems especially suitable for cross-fertilisers by taking into consideration inbreeding depression and heterosis. Much of the commercial breeding of Brassicas in Britain is still at the first stage. In some horticultural crops where large size may mean coarse quality, hybrid vigour seems unnecessary and inbreeding is being examined as a method of securing greater uniformity of type. In the swede self-fertility seems to be a disadvantage for two reasons. It is a hindrance to the production of $F_1$-market seed, and it is not sufficiently flexible for the breeding of British strains where a great many details of colour and shape have to be included in an ideal type. By the time the yielding capacity has been determined, say the $F_4$-generation, the type is too fixed to respond to selection for fancy points. In Den-

mark, on the other hand, dry matter yield has been the criterion of worth since the 'eighties, and the swede is grown to provide this where conditions are unsuitable for fodder-beet. The breeding of the two crops has followed the same pattern except that hive bees had to be used in the swede propagating houses to obtain as much intercrossing as possible. The story of the early history of root crop breeding in Denmark was given by FABER (1920); and probably the most up-to-date account is a chapter in English in the new edition of Handbuch der Pflanzenzüchtung (not yet seen). Having first determined by yield trial that the "Bangholm" variety of swede gave the greatest yield of dry matter, all other varieties were discarded. Strains of Bangholm which were at first mass-selected, were tested in yield trial and all but the best discarded. Pursuing this policy the swedes grown in Denmark became extremely efficient yielders of dry matter. When it was found that the yield could be increased by heterosis, the aim became strain-building by crossing for the production of $F_1$-market seed. Families or lines were now multiplied separately and to some extent inbred, and were mixed in the crop from which the market seed was taken. This suits a self-sterile crop, such as the mangold, better than the swede where considerable selfing occurs.

With the change of emphasis to outcrossing in the market seed, it was no longer the yield of the progeny of a family that was important but rather its ability to combine with unrelated plants to give high yielding offspring. K. J. FRANDSEN (1952), who with H. F. Frandsen elaborated the polycross system of strain testing, lists four methods of testing mother plants, (*a*) after free pollination, (*b*) after top-cross, (*c*) after polycross and (*d*) after diallel cross. He points out that while the diallel cross will give the most uniform basis of comparison of a small number of parents, the polycross is more useful in the first cycle when there are large numbers to be tested. K. J. FRANDSEN (1956) later outlined a scheme for breeding species in which formation of clones is difficult.

It should be noted that the polycross test may be applied either to individual plants or to larger units. With perennial forage plants that are easily cloned, the individual genotype may be under examination. This could also be applied to some Brassicas if seed production was on a relatively small scale and the price of seed would justify the laborious propaga-

tion by cuttings. In root crops where cloning is impracticable, families or lines, each containing a diversity of genotypes, though relatively inbred, may be mixed for the propagation of market seed. It is the combining power of these families that is tested by polycross, and sufficient mother plants have to be included to give a representative sample of the family. The polycross must necessarily be on a very much smaller scale than the multiplication of market seed where thousands of plants are flowering together. Greater uniformity of genotype may, however, be possible in the lines from which market seed is hybridised. Thompson (1959) has suggested a procedure for obtaining double-cross hybrid seed of kale, on an economic scale, from relatively true breeding lines obtained by selfing selections from commercial stocks by bud pollination.

*Contamination of Strains.*—Where the districts suitable for propagation of seed are relatively small, as in Britain, the problem of isolation of seed crops is serious enough, but where oil-seed crops are grown it must be intensified. Distance isolation is necessary to separate a seed crop of a variety not only from other seeding crops of that species but from any other Brassica that can cross moderately easily with it. This aspect has received much attention since the classical work of A. W. Sutton (1908 : Y232). Nelson (1926 : Y165) analysed contamination into its components ; the self-compatibility of the one crop and the cross-compatibility between the two ; both these being affected by non-hereditary factors, such as distance, size of crops, age or condition of the female plant. Bateman (1947) assessed the distribution of contamination in insect pollinated crops using radish and turnips, and found a rapid fall from in one case 60 per cent at 20 ft. to 13 per cent at 80 ft. but there was still 6 per cent at 140 ft. and 1 per cent at much greater distances. In a later study Bateman (1951) observed the taxonomic discrimination of bees, finding that their short distance flights on a foray showed constancy of species and even of varieties. The long flights of the bees could not be followed, and it was assumed that they started or concluded the foray. Occasionally, unexpectedly severe contamination ruins a seed stock. This does not become apparent until the following year, and the causes are then very difficult to establish ; indeed they are sometimes the subject of a lawsuit. Swede-like rape is a frequent source of contamination in swede, usually as a true rape plant, sometimes as an $F_1$-hybrid and

occasionally as $F_2$-segregates. The last are possible because the market seed is produced in two stages, stock seed from selected plants and a multiplying generation of a late summer sowing, in which, however, rape or hybrids could be detected by flower colour. One case of contamination was reported as having occurred between small seeding plots of swede and a *B. napus* form of rape-kale, which a farmer was propagating for his own use a quarter of a mile apart ; both crops were contaminated, the swede having 6 per cent of hybrids. Possibly in a case like this the plots are so sited that the bees are induced to visit both in one foray.

Many workers have examined the crossability of species and forms. Sinskaya (1927 : Y221) classified the hybridisations between Brassica species according to ease of seed production. Tedin (1931) investigated the dangers from crossing in the seed production of turnips, and Okonogi (1934) observed contamination of stocks of *B. napus* and *B. pekinensis*, finding that the small hybrid seed could be separated from each species by sieving. Calder (1937 : Y25) examined the possibilities of contamination between Brassicas seeded in New Zealand, and the writer attempted to outline the position in Britain in 1939 (Y38). Thomas and Crane (1942) made a cytogenetic classification of Brassica crops, the results of which were presented to horticulturists (Crane 1943 : Y32). Seed Growers Lea et No. 1 (at present under revision) issued by the National Institute of Agricultural Botany also contains instructions about isolation.

Relatively little is known about the degree of cross-pollination occurring in crops where some or all the plants are self-fertile. In swede-rape some plants are 100 per cent cross-fertilised, but the mean cross-pollination is 36 per cent, and about 30 per cent for self-fertile plants (Olsson and Persson 1958), on the other hand, white mustard was found to be 99.6 per cent self-pollinated (Olsson 1952). Tedin and Nissen (1932) studied pollen distribution in a flowering field of swedes. Seed crops are affected to various degrees by infestations of pollen-beetles and weevils, and these together with the frequency of bees may vary the proportions of selfed and crossed seed.

An autotetraploid may hybridise with species which are quite incompatible with its diploid parent stock. This has been found in sarson by Tandon (1952).

*Vegetative propagation*.—For various reasons the extension of the life of plants is becoming more and more necessary in *Brassica* breeding. A plant may be kept until information of a progeny test is available, or to supply information as to incompatibility when crossed with its offspring. A male-sterile plant may be reproduced in quantity by cloning, or a horticultural form, such as cauliflower, may be difficult to seed without vegetative propagation, if it has been grown under normal conditions for selection (Jensma, 1957). Where side shoots are absent or modified as in brussels sprout, several methods including root cuttings have been devised by North (1952, 1953), while Haine (1951, 1955) has perfected a technique for propagating cauliflower from pieces of the curd, and delaying flowering by growing the cuttings in a temperature of not less than 20° C. Another method of propagating cauliflower is from root-shoot cuttings (Nieuwhof 1958) ; adventitious buds are induced on roots which are still attached to the selected plant.

*Genetically-superior individuals*.—Taking yield of dry-matter in the ' bulb ' as the criterion for the selection of swedes, is it possible to detect genetically superior individuals in a mixed or segregating population ? Bulb weight is subject to extreme modifications. Individual weights range from a few ounces to five pounds or more even where spacing is regular. Selection of large plants does tend to perpetuate heavier cropping types, though the mean differences in yield trial of (selfed) progenies are small. Selection of plants showing high dry-matter percentage without regard to weight will tend to isolate small-rooted high dry-matter percentage types. If the records are plotted in a correlation table it will be seen that a strong negative correlation (about $r = -0.6$) exists, and few plants fall in the high/high classes. If these are selfed, it is usually found that one or other character was not inherited in the progeny, and that the parents were not genetically superior.

Powers (1957) has presented methods and formulas used to identify genetically-superior individuals and to predict genetic gains in segregating and heterogeneous populations. To illustrate the application of these methods he examined the weight of root and percentage sucrose in sugar beet. His trials were extensive, six strains in 20 and four in 60 complete randomised blocks ; the plants widely spaced (40″ × 20″) to minimise competition, and each culture reduced to 12 plants

at singling of which 8 disease-free specimens were used for estimation.

The immediate genetic theory and the methods of predicting genetic gains had to do with the partitioning of variance into its components and the partitioning method of genetic analysis. The measure of *environmental* variability was provided by two treatments, a line of beet inbred for many generations, and the $F_1$-hybrid seed of two such lines. For percentage sucrose the distributions and variances of these two were practically identical, there being no heterosis, and either variance could be deducted from the variances of the more heterogeneous treatments to measure the genetic variance of the latter. Weight of root is a character affected by heterosis, and here the variance is positively related to the mean weight, which was low in the inbred line and high in the $F_1$. On the data of these two a regression was calculated from which the environmental variance appropriate to each segregating strain could be computed. The identification of individuals genetically-superior and the prediction of genetic gains depends on the determination of an upper class (in the distribution) beyond which the odds are great that individuals will not occur due solely to environmental variability. This was done for each character separately and small percentages occurred above the assessed class in the more heterogeneous strains.

Powers then considered both characters simultaneously, as is essential in breeding, and in one strain where 3.7 per cent of the population had been identified as genetically superior for percentage sucrose and a different 2.5 per cent for weight of root, he calculated that the proportion of the population that might be expected to exceed the upper class limits for both characters would be the product of probabilities, 0.000925, or about one in 1,000. But this assumed independence of the characters, which was not the case in this strain, where a significant negative covariance existed. In fact, Powers concluded that no individual genetically superior for both characters could be expected in a population of 24,000 plants, though he suggested a method of finding them by several stages of selection and re-selection from progenies. This work is mentioned in some detail because selection of widely spaced transplants is practised in Brassica breeding.

*Conclusion.*—This article embodies a report which the writer was instructed to compile in connection with a revision of the

*Brassica* research programme. The questions were : what has been done and what remains to be attempted ? On examining the literature it becomes obvious that Dr Yarnell in his Review has given a complete answer to the first question to within a few months of 1956. His method was to give cytogenetical information under the headings of cultivated forms or species, and of hybridisations arranged according to the parental chromosome numbers. Such treatment, while excellent for detail, gave him relatively little opportunity for generalisation. The present article attempts to outline what has been happening in the *Brassiceae* as a whole, though too often this reverts to discussion of the smaller group which interests the European breeder. If too much space has been devoted to cytological discoveries it is because polyploidy in one form or another has already become an established method of breeding, and because other devices such as exchange of single chromosomes may become available in the future.

There are other fields of work which have not received here the attention they merit. The quest for genetical information goes on ceaselessly, and though there have been few spectacular advances since the 'thirties, there must be much information in the literature which could be assembled. A great deal of strain testing and breeding is carried out in connection with investigations on plant pathology, animal nutrition and other economic problems.

## Summary

An attempt is made to sketch the achievements of geneticists, cytologists, breeders and others working on cultivated forms of the *Brassiceae*. Much information has been gained about compatibility within and between forms, inheritance, disease resistance and economic capabilities. Greater co-ordination of results, especially of work done by Japanese and Western cytologists and breeders might be desirable. The fruits of their endeavours in the form of synthetic amphidiploid and autotetraploid strains are beginning to benefit Agriculture.

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## THE 1958 INTERNATIONAL CODE OF NOMENCLATURE FOR CULTIVATED PLANTS

The International Committee on Horticultural Nomenclature and Registration prepared an International Code of Nomenclature for Cultivated Plants which was published in 1953, a Code formulated primarily by those interested in horticulture, though it was soon apparent that there was a desire on the part of agriculturists and foresters to see how far such a Code could be made equally applicable to agricultural and sylvicultural plants. This desire was given practical expression when, at the Fourteenth International Horticultural Congress held at Scheveningen in 1955, it was decided to ask the International Union of Biological Sciences whether the composition of the Commission for the Nomenclature of Cultivated Plants, which they had set up in 1948, could be so revised as to have an adequate representation of agriculturists and foresters as well as horticulturists. The Union agreed to this request and in due course the Commission's membership was enlarged to twenty-four, with approximately equal numbers representing agriculture, forestry and horticulture.

Dr R. de Vilmorin was appointed the Commission's president, with Mr J. S. L. Gilmour rapporteur and Dr H. R. Fletcher secretary and the following representing agriculture :—

Dr J. W. Gregor—Scottish Plant Breeding Station, Pentlandfield, Roslin, Midlothian, Scotland.

Mr F. R. Horne—National Institute of Agricultural Botany, Huntingdon Road, Cambridge, England.

Dr P. S. Hudson—Commonwealth Bureau of Plant Breeding and Genetics, Cambridge, England.

Dr Jorge León—Plant Industry Department, Inter-American Institute for Agricultural Science, Turrialba, Costa Rica.

Dr G. Nilsson-Leissner—Swedish State Seed Testing Station, Stockholm 19, Sweden.

Dr F. E. Nijdam—Stichting voor Plantenveredeling, Nude 66, Wageningen, Netherlands.

Dr B. P. Pal—Indian Agricultural Research Institute, New Delhi, India.

Mr T. A. Russell—Royal Botanic Gardens, Kew, Richmond, Surrey, England.

Dr E. N. Sinskaya—Institute of Plant Industry, Herzenstreet 44, Leningrad, U.S.S.R.

Dr M. G. Weiss—Field Crops Research Branch, U.S. Department of Agriculture, Beltsville, Maryland, U.S.A.

The new Commission held its first meeting in 1956 at the University of Utrecht. In the following year a second meeting was held in London, and on the basis of decisions taken at this meeting the Code was prepared for publication in 1958 by an Editorial Committee, Drs Hudson, Nilsson-Leissner and Nijdam representing agriculture.

# THE SIGNIFICANCE OF THE INTERNATIONAL CODE OF NOMENCLATURE FOR CULTIVATED PLANTS TO INTERNATIONAL TRADE IN HERBAGE CULTIVARS.

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The growing interest of farmers and seedsmen in new varieties of crop plants and the frequent exchange of varieties between different countries have drawn attention to the great importance of the names which are given.

In the first place the term ' variety ' itself is unfortunately confusing because it has been used for a long period by botanists to embrace wild forms below the level of a species. The Code therefore recommends that the unit for crop plants should be the ' cultivar.' It is however, recognised that the old term ' variety ' cannot be immediately dropped, but wherever names of cultivated plants are listed, these should be formally designated as *cultivars* so as to prevent confusion with the wild plants.* Cultivated plants are no less in need of some agreed system of naming than the wild species because new cultivars are being deliberately produced at plant breeding stations all over the world apart from the local races of cultivated plants which are being discovered in the course of agricultural research and advisory work. The purpose of the Code is to provide a guide to plant breeders and others who wish to name cultivars, and so to promote uniformity, accuracy and fixity in the naming of cultivated plants.

Only by following the simple principles in the International Code can confusion be avoided in future years as the number of new cultivars (varieties) increases.

The Code emphasises the importance of registration as a means of stabilising names. Registration is simply the acceptance of a cultivar name by an official registration authority and the inclusion of this name in a register ; it does not imply

* The International Code of Nomenclature for Cultivated Plants is concerned with the " fancy " naming of cultivars ; the use of scientific (" Latin ") names for both cultivated and wild plants is governed by the International Code of Botanical Nomenclature.

judgment on the distinctness of a cultivar from others. In other words a name can be legitimately given to a cultivar without having to establish its distinctness from all others, though, of course, it is assumed that registration authorities will not knowingly give distinctive names to cultivars that are not in some respect differentiated from each other.

While registration is an essential first step, it can readily be appreciated that registration unaccompanied by description is not in itself sufficient to satisfy agricultural needs. The Code takes this need into account and now descriptions must be associated with cultivar names. In the case of agricultural crop plants it is most desirable that descriptions be compiled from test data, and although the registration of names is independent of testing the Code recommends that when possible tests should precede registration. When contemplating the problems of description of herbage cultivars from test data it is well to draw a distinction between tests of agronomic performance conducted under actual agricultural conditions, and tests designed with the object of collecting data for descriptive purposes. The former type of test, apart from inherent technical difficulties, takes a long time even to cover a fraction of the infinite variety of agronomic environments, but the time factor is not of such vital importance as it is in the latter. Tests, however simple, which take so long to complete that stocks of cultivars are either lost or find their way on to the market under unregistered names before the descriptive information becomes available defeat their own purpose. Equally defective are tests involving techniques so elaborate or so costly that only a fraction of the available cultivars can be handled.

At the present time opinions differ widely not only as to what attributes should form the basis of cultivar description, but also in regard to the techniques to be adopted for the measurement of these characteristics. In fact so varied are the techniques under which current herbage plant tests are conducted that it is seldom possible to compare the findings of one investigator with those of another. To facilitate the direct comparison and interpretation of descriptions founded on test results, and so promote the intelligent exchange of cultivars between countries, it is now quite apparent that some degree of international standardisation is necessary both in respect of the characters to be described and of the techniques employed for their assessment.

The indirect evaluation of the attributes of herbage cultivars by way of animal responses has an appeal to those who feel that the ultimate product of grassland, the animal, ought to be the criterion of cultivar worth. But while for certain purposes this attitude has much to commend it, to base descriptions of cultivars on animal performance offers a somewhat unrealistic approach, especially as different practices employ animals of many kinds and in many different ways. In fact considering agronomic conditions in general the range of possible environments under which tests might be conducted is so great that to conduct tests in all of them is an impossibility. If, on that account it is accepted that the purpose of a description is to provide an estimate of a cultivar's potential rather than proven suitability for particular agronomic practices, then it is not a very revolutionary step to accept the idea of conducting tests under conditions which have no exact replica in agriculture. Such an approach paves the way to a purely botanical assessment and the adoption of test techniques amenable to standardisation.

Assuming that the results of tests will be expressed in strictly botanical terms the next step is to consider the choice of attributes of descriptive value and also the techniques appropriate for their measurement.

In the description of a cultivar for the guidance of farmers and others, characters which may have a bearing on its suitability for particular kinds of agronomic environment deserve special consideration. Moreover since time is important the characteristics chosen must be those that are capable of being relatively rapidly evaluated. Maturity type is an obvious first choice because early and late maturity cultivars play very different agronomic roles and the use of the wrong type can have serious economic consequences. A characteristic intimately related to maturity type and of equal agronomic significance is the seasonal rhythm of production. Habit of growth involving plant size and form is another character which has a bearing on the way a cultivar can be used. Then from the standpoint of seed production, and to a less extent of agronomy, cultivar variability ought to be taken into account. Where resistance to a specified race of a pathogenic organism happens to be definitely known this information should be mentioned in the official description ; generalised statements regarding ability to resist disease should be accepted with considerable caution.

Of the characters mentioned maturity type, growth-habit and variability can best be assessed in spaced plant trials, but for the determination of growth rhythm as measured by yields taken at intervals over the growing season it is desirable to employ a sward technique. It is true that yield data can be obtained from spaced plants, but although there is considerable correspondence between the data obtained from spaced plants and swards when certain growth habits are involved, other growth habits give very contradictory results. The two techniques serve different purposes and while the spaced plant tests can be relatively easily standardised, standardisation of a sward trial requires agreement in respect of such treatments as the method of cutting and levels of manuring.

Since under different environments the same inherited attributes are liable to be expressed differently it follows that a description based on regional field test data is not equally valid everywhere, though in so far as responses to certain specific environmental factors are concerned it should be possible for controlled laboratory tests to yield information of universal significance. Although the relative agronomic values of cultivars cannot directly be deduced from botanical descriptions such descriptions, especially when compared with those of control cultivars of established agronomic reputation, should provide a reasonably reliable indication of the probable suitability of new cultivars for particular agronomic environments. It is not suggested that descriptive tests should replace agronomic tests, but that it would be sensible when choosing cultivars for agronomic evaluation to give priority to the cultivars which are used as controls in descriptive tests because it is evident that not every described cultivar is likely to be submitted to official agronomic tests—*i.e.*, to tests involving treatments of the kind found in actual farming practice.

As the number of herbage cultivars increases, the importance of tapping world supplies will become increasingly appreciated and the demand for the regional reassessment of the characteristics of foreign cultivars will almost certainly arise. When the number of native and alien cultivars available for use in any given territory is large there will be a tendency for the native controls to form focal points around which cultivars possessing common features of importance to cultivators will group themselves. The International Code makes provision for assemblages of similar cultivars within a species to be

classified as *groups*. It might be of practical convenience to agriculturists to have the characteristics of similar cultivars summarised in this way, but such classifications though regionally meaningful would inevitably vary from region to region. For instance, in *Lolium perenne* a grouping based on maturity class might be of especial importance to farmers in one country, whereas habit of growth (indicating hay or pasture type) might be of greater significance in another. Moreover in two countries which adopt the same criterion of maturity, a cultivar might belong to the early group in one and to the second-early in the other.

Turning now from the registration, testing, description and classification of cultivars to the authorities which are given the responsibility of undertaking these tasks. According to the International Code an official registration authority is "any international or national organisation or agency so designated by appointment or by agreement with those concerned." It is the hope of the Nomenclature Commission that official registration authorities will be set up as rapidly as possible to cover all the major cultivated crops. In Appendix ii of the Code is given a list of international authorities each covering an extensive genus or group of plants. In the case of crops for which descriptions are drawn up after tests conducted by an official testing authority it would seem sensible that such testing authorities should also act as official registration authorities. In that event since testing can most usefully be organised on a national or provincial basis, it follows that registration should be similarly organised. A national or provincial authority would then be responsible for registering the names together with the relevant descriptions of those cultivars which happen to have *originated within its own territory*. In addition to the formal requirement to register native cultivars it would have obvious advantages if each national authority was also responsible for maintaining a list of the names and descriptions, amended where necessary, of all alien cultivars which have passed through the official national tests. Thus national authorities would be in a position to publish authentic cultivar descriptions for the information of advisory officers and farmers within their spheres of influence.

However, in order to publicise world cultivar resources some kind of international agency would still be needed. To permit such an agency to fulfil this important function it would have

first to be notified of the existence of national authorities and, secondly, to receive from them the names, with descriptions, of the cultivars which they themselves have registered. But just how cultivar information will from time to time be circulated internationally will depend on the volume of work involved. For instance, after the appropriate translations have been made, national lists might be distributed as they stand ; or perhaps, instead of publishing descriptions in full the information could be condensed by grouping cultivars with similar descriptions and employing classificatory headings ; alternatively the national lists might be shortened by excluding those cultivars which do not happen to be covered by seed certification schemes, for when all is said and done the practical usefulness of publicising registered cultivar information will largely depend on *authentic* seed stocks being currently available to commerce.

Where the plant breeder is multiplying and distributing seed of his own new productions, the resulting stocks are likely to be true to the description on which the cultivar name was first given. In the course of multiplication by other seedsmen and farmers, the cultivar may, however, lose its character or it may become mixed with other cultivars. This is particularly true of the herbage plants most of which normally set their seed by cross-pollination either within the seed crop or with pollen from adjoining seed crops.

The best safeguard for seed produced by anyone other than the breeder, is through a scheme for seed certification. By means of checks on the basic seed sown for multiplication, the conditions in the seed crop and during handling in the granary, the grower can be assured of buying what he wants. Moreover, since the acceptance of a cultivar for seed certification involves choice by a certifying authority, seed certification schemes have the incidental merit of providing what are in effect lists of " approved " cultivars ; registration of a cultivar name, on the other hand, is not in itself evidence of official recommendation.

In Britain and in many other countries, national schemes of seed certification have been developed. Recognising the growing importance of International trade in seeds, the organisation for European Economic Co-operation (O.E.E.C.) has sponsored work between the different European countries. Through its European Productivity Agency (E.P.A.) the O.E.E.C. has made a study of existing arrangements for the

certification of herbage seed throughout western Europe, and by correspondence with some other countries such as United States of America and New Zealand. In discussions with representatives of the different countries a scheme has been drawn up under which herbage seed may be sold with a special International label. This is done after the country concerned has published an account of the technical standards employed and has given an undertaking to obtain " basic " seed direct from the breeder and to check the final product. It is unnecessary to point out that valuable varieties of herbage plants may be useful far outside the national boundary. The O.E.E.C. scheme known as E.P.A. Project 215 will enable farmers in any country to buy seed of which they can be sure : in this way the control of herbage seeds is ahead of that in any other group of crop plants.

Grass is the most important crop in most of the north European countries and the arrangements for describing new varieties, and for producing absolutely reliable stocks of seed are likely to be of the greatest value to the agricultural industry

# THE ASSESSMENT OF GRASS STRAINS AT EAST CRAIGS

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The increasing appreciation within the farming industry of the distinctive merits of strains of grasses, both regional and bred, and the entry into commerce of large quantities of seed of such strains, have emphasised the need for some machinery for their evaluation. As the published evaluations are not always related to local conditions, it is obvious that assessment work must be carried out in Scotland, and, as tests of various kinds and in different places are required, a co-ordinated national system is necessary. It was considerations such as these that led to the organisation after the war of two types of trial in Scotland, one designed to supply fundamental botanical information about strains and the other designed to supply agronomic information. The fundamental work, together with overall collation, was undertaken by the Scientific Services of the Department of Agriculture and the agronomic work by the three agricultural colleges.

The botanical studies carried out by Scientific Services at East Craigs have in the main followed the spaced-plant method, but use has also been made of the vernalisation procedures devised for ryegrasses by Cooper (1956). It should be emphasised that spaced-plant studies are not the last word in strain assessment. Such studies provide a relatively cheap method of classifying a large number of strains in a preliminary way, but they have their limitations and have to be followed up by sward trials. The resources available for sward trials are limited and the relatively few strains that they can accommodate, and their controls, can be effectively selected by consideration of data derived from spaced plants. If spaced-plant studies are made too complex by the measurement of too much, some of their virtue disappears; their essence lies in the simplicity and quickness of measurement of the characters chosen for assessment.

The International Code of Nomenclature for Cultivated

Plants that has been negotiated and is now generally accepted, attaches considerable importance to the official registration of cultivars and registration must be accompanied by description. At their inception, the spaced-plant trials at East Craigs were regarded as an essential preliminary to the sward trials of the Colleges, but it is now clear that they can play a vital part in the registration of grass cultivars by providing the requisite descriptions. Registration cannot await the accumulation of agronomic data that may be necessary for the full evaluation of a strain. The descriptions derived from spaced plants are restricted in scope, but they are adequate for the allotment of a new strain to a type and they become available relatively quickly. It is therefore planned that inclusion in these trials shall be an integral part of the procedure organised jointly by the National Institute of Agricultural Botany and the Department of Agriculture for Scotland for registering a grass strain in the United Kingdom.

The East Craigs staff had a practice run with the spaced-plant method in 1949-50 and the first formal trial was planted out in 1950 for assessment in 1951. A trial has been planted out each year since (Thomson and Seaton, 1956 *a* and *b*, 1957 ; and Thomson and Keppie, 1957, 1958), and the method of planting and the layout have become a routine. Each trial requires two years, assessment and measurement of the plants being carried out in the year after planting. So as to cover a range of weather conditions each trial is normally grown three times in successive years ; this was not always possible in the early years, but it is hoped that in future each strain will go through a series of three trials.

Seed is sown in John Innes seed compost under glass in late April or early May and, after hardening off, 54 seedlings of each strain are planted out in June or July. The most effective way of doing this is to sow 2 seeds in a whalehide tube, such as is used for sweet peas, and if both germinate one seedling is removed. Subsequent thinning and transplanting are thus avoided and the tubes are planted intact in the plot.

The randomised block layout is used with 6 replications, each block containing a row of 9 plants from each strain under test. The spacing is 30 inches between plants and 36 inches between rows ; this gives each plenty room to develop and obviates edge effects.

Statistical analyses are made of the variation in each character :

(*a*) between strains in each trial separately ;
(*b*) between strains, taking all trials in the series together ;
(*c*) between trials for each of the strains separately ;
(*d*) between trials for all strains taken together.

For this purpose, statistical treatment is by analysis of variance, taking the average measurement or score of the nine plants comprising a row as the unit. However, in calculating the variance within a strain in order to compare its variability with that of another strain, the individual plant is taken as the unit.

Seed is normally obtained from the breeder of the strain. In the early years, fresh seed was obtained each year, but the procedure now is to obtain enough seed in the first place for three years, keep it in dry cool conditions and sow part of the same seed each year.

The characters measured or otherwise assessed in each plant in the year after planting are of four kinds :

(*a*) Date of ear emergence.
(*b*) Habit of growth.
(*c*) Size.
(*d*) Frequency of shoots in the aftermath.

*Date of Ear Emergence.*—Date of ear emergence is determined by inspecting each plant twice a week from April onwards and noting the date on which at least 3 inflorescences have become visible. The date has been found to be extremely variable, not only from year to year, but also from plant to plant. Presentation of results is simplified by referring them to a control strain as a base—*e.g.*, perennial ryegrass strains are described as shooting so many days before S.23.

The agronomic value of shooting date depends in part on the extent to which earliness as measured in this way is indicative of the early spring growth so valued on the farm. It has been shown that in perennial ryegrass, earliness of spring growth is closely correlated with earliness of shooting (Heddle *et al.*, 1950), and this is borne out by the figures in Table I. The same correlation is shown by Cocksfoot, but is not at all well marked in Timothy. In general, an early shooting date

can be taken as indicating the probability of early vegetative growth, but it is not conclusive and exceptions are to be expected.

## TABLE I.

Relative Ear Emergence dates and increases in shoot length during April, of spaced plants of control strains. Perennial Ryegrass and Cocksfoot average figures, 1956-58; Timothy average, 1956-57.

| | Ear Emergence Date—Days | April growth —cms. |
|---|---|---|
| Perennial Ryegrass— | | |
| Irish | − 28 | 7 |
| S.24 | − 24 | 8 |
| S.101 | − 3 | 6 |
| S.23 | 0 | 5 |
| Cocksfoot— | | |
| S.37 | 0 | 7 |
| S.26 | + 8 | 6 |
| S.143 | + 11 | 5 |
| Timothy— | | |
| Scotch | 0 | 11 |
| S.51 | + 7 | 11 |
| S.48 | + 7 | 9 |

*Habit of Growth.*—Habit of growth has been assessed at 3 developmental stages—at the start of spring growth, at ear emergence and at anthesis, but in general, differences in spring growth habit have been so slight that this assessment has been dropped.

Habit is assessed by the use of a series of profile drawings typifying a range of growth habit from prostrate to erect. As an example, the profiles used for Timothy are shown in Fig 1. For the ear emergence habit there are 5 profiles and for the anthesis habit, 7 profiles. A score is allotted to each profile, ranging from 1 for the most prostrate to 5 or 7 for the most erect, indicating the degree of erectness. Each plant is compared with the profiles and given a score according to the one it most closely resembles and an average score is calculated for each row of 9 plants and subsequently for each strain.

FIG. 1. GROWTH HABIT AT EAR EMERGENCE (ABOVE) AND AT FLOWERING.

Some may boggle at the idea of treating statistically figures obtained in this way and might prefer more conventional measurements as indices of habit. Measurements have in fact been made of height/width ratio and of the angle subtended by the outer shoot at the time of ear emergence and average figures for the control strains are set out in Table II., with figures obtained by using profiles for comparison. The agreement is good enough to justify the use of the profile method. On the whole the ratios agree rather better with the profiles than do the shoot angles and in practice the latter feature is a somewhat imprecise one to measure. A rapid method of measuring the ratio has now been evolved and as this method is more readily devolved on to junior staff than is assessment by profile, its adoption in future trials is under consideration.

*Size.*—Two measures of the size of each plant have been taken at the stage of anthesis. Stem length is measured by taking the length of the longest shoots. This is not necessarily the same as the height of the plant ; the largest stems occur in the most erect plants in Cocksfoot, but in the most prostrate ryegrass plants, while in Timothy no association between growth habit and stem length has been found.

In the early trials, after the measurement of stem length the plants were cut down in a uniform manner and the green material weighed on the spot and this was taken as a measure of size. The figures obtained, however, were so variable from year to year and so dependent on the date of anthesis that this measurement has been abandoned.

## TABLE II.

HABITS OF GROWTH AT EAR EMERGENCE OF CONTROL STRAINS AS ASSESSED BY THREE METHODS. AVERAGE FIGURES, 1956-57.

| | Profile | Height-Width Ratio | Angle of outer shoot (Degrees) |
|---|---|---|---|
| Perennial Ryegrass— | | | |
| S.24 . . . | 3.1 | 0.7 | 43 |
| Irish . . . | 2.8 | 0.6 | 36 |
| S.101 . . . | 2.7 | 0.6 | 39 |
| S.23 . . . | 1.8 | 0.4 | 26 |
| Cocksfoot— | | | |
| S.37 . . . | 2.8 | 0.9 | 45 |
| S.26 . . . | 2.6 | 0.9 | 41 |
| S.143 . . . | 1.8 | 0.6 | 28 |
| Timothy— | | | |
| Scotch . . . | 3.2 | 1.9 | 64 |
| S.48 . . . | 2.9 | 1.5 | 64 |
| S.51 . . . | 2.9 | 1.5 | 61 |

*Frequency of shoots in the aftermath.*—The tendency of a grass to throw up flowering shoots after a hay-cut is an important agronomic character. In Cocksfoot swards few shoots develop, but in perennial ryegrass and Timothy there are marked differences between strains in this respect.

It has proved a difficult character to evaluate but consistent results have been obtained by scoring each plant against a series of 5 diagrams ranging from " very few heads and leafy " to " many heads and stemmy." The diagrams used for Timothy are shown in Fig. 2.

FIG. 2. RANGE OF AFTERMATH SHOOTING.

*Control Strains.*—Each trial has included control strains of each species, either well-known regional strains such as Irish Perennial Ryegrass and Scotch Timothy or strains bred at

Aberystwyth. The average figures found for three characters in the control strains in two 3-year periods are given in Table III.

## TABLE III.

VARIABILITY SHOWN BY CONTROL STRAINS—
AVERAGES FOR TWO 3-YEAR PERIODS

| Species | Control Strain | Date of Ear Emergence | | Ear Emergence Habit | | Aftermath Shooting | |
|---|---|---|---|---|---|---|---|
| | | 1953-55 | 1956-58 | 1953-55 | 1956-58 | 1953-55 | 1956-58 |
| Perennial Ryegrass | Irish . | 16 May | 14 May | 3.4 | 2.9 | 3.6 | 4.4 |
| | S.101 . | 8 June | 8 June | 3.0 | 2.6 | 2.2 | 1.4 |
| | S.23 . | 11 June | 11 June | 2.3 | 2.0 | 2.0 | 1.3 |
| Timothy . | Scotch | 12 June | 12 June | 3.6 | 3.4 | 5.1 | 5.2 |
| | S.48 . | 20 June | 20 June | 3.3 | 3.1 | 4.8 | 5.0 |
| | S.51 . | 20 June | 19 June | 2.8 | 3.0 | 4.6 | 4.5 |
| Cocksfoot | S.26 . | 14 May | 23 May | 3.2 | 2.7 | 1.5 | 1.4 |
| | S.37 . | 17 May | 15 May | 3.4 | 3.0 | 1.5 | 2.0 |
| | S.143 . | 16 May | 27 May | 2.9 | 1.9 | 1.5 | 1.7 |

The consistency in ear emergence date of the ryegrass and Timothy controls is remarkable. Emergence date varies from year to year, but apparently 3 years is a long enough period for these variations to cancel each other out. These dates provide good evidence, too, of uniformity in the material sown over six years. It is of interest to note, however, that habit of growth and aftermath shooting do not show the same uniformity. Particularly in perennial ryegrass, differences between 3-year periods are of the same magnitude as differences between strains, but in each period the ranking of the strains is in the same order. Apparently, a 3-year period is not long enough to smooth out this variability and it is important to judge a strain not only on the figures that emerge from these trials, but also as it compares with the control strains.

Of the Cocksfoot strains S.37 has been uniform in ear

emergence date, but S.26 and S.143 have varied both absolutely and relatively. It is known that S.143 has varied owing to the reconstitution of the strain.

*Interpretation of Results.*—The results obtained in this work so far, have emphasised that the key characteristic of a grass strain is the relative earliness or lateness of ear emergence. It is true that within a strain individual plants differ widely in their emergence dates, but nevertheless, the average date is characteristic of the strain. The agronomic significance of the character lies in its correlation with other growth features, one of which, spring growth, has already been mentioned.

In spaced-plant work the most pronounced correlation is with habit of growth—the later the emergence date the more prostrate the growth. Presumably a late emergence allows a longer period for the multiplication of tillers and the consequent horizontal spread of the plant, though exceptional strains may fail to tiller well and thus show a less prostrate habit than would be consonant with their maturity. The general correlation holds, however, in the three species studied —perennial ryegrass, Timothy and Cocksfoot.

Stem length increases up to the time of anthesis. In perennial ryegrass, strains tend to anthese in the same order as their inflorescences emerge but at longer intervals. Late-emerging strains therefore have a longer time for stem elongation. In Cocksfoot, however, all strains tend to anthese simultaneously when weather conditions are suitable, thus affording less time to late emerging strains for stem elongation, and they consequently have shorter stems than early strains. In Timothy differences in stem length, between the strains studied have been slight.

The weight of a plant at the time of anthesis is also influenced by the time available for growth and is thus influenced by emergence date.

In the climatic conditions of this country, the factor which in practice determines the ear emergence date of a grass strain is daylength. Early strains of perennial ryegrass and Timothy have a relatively short day requirement and after cutting, tillers which are either too short to be damaged or which develop subsequently still find the daylight suitable for flowering and abundant shoots emerge in the aftermath. Late-emerging strains do not shoot profusely in the aftermath because the hay-cut is taken after midsummer and daylength is then too short for floral initiation ; temperature is a sub-

sidiary factor in perennial ryegrass. Cocksfoot has a definite low temperature requirement for flowering, in addition to its daylength requirement; this prevents any more than an occasional plant from shooting in the aftermath and the correlation between emergence date and aftermath shooting does not apply. The perennial growth of a grass is also linked to its emergence date, though this is not obvious in the short duration of a spaced-plant trial. Tillers die off after flowering and the perennial growth of a grass depends on the vegetative tillers that are left in the autumn; these, not having flowered, persist over the winter and form the basis for the next season's growth. In late-emerging strains of perennial ryegrass and Timothy, there are more vegetative tillers left than in the early strains and consequently they have a better chance of survival.

Because of its effect on nutritional value the leafiness of a grass strain is an important agronomic characteristic. It has not yet been possible, however, to devise a method of assessing this character directly that is suitable for spaced-plant work. Leafiness is largely dependent on ear emergence date. Late strains are more leafy over the season than early strains, because they do not run to stem until later and then produce few inflorescences in the aftermath. That, however, is not the whole story; some strains which emerge about the same time differ in the stemminess of their aftermath—*e.g.*, Irish and S.24 ryegrass. These factors affecting leafiness are studied in spaced-plant trials, but any differences there may be in the leaf/stem ratio of plants in full flower, for example, have so far gone unassessed.

The emphasis placed on emergence date may suggest that this is the only character worth observing and that all other features could be ignored. While the general proposition holds that if you know the maturity of a strain you know all, there are exceptional strains which do not conform. Thus Scotia Cocksfoot combines earliness with a relatively prostrate habit, Ca 571 ryegrass combines lateness with erect growth and S.24 ryegrass has an exceptionally leafy aftermath for an early grass. In future developments, particularly for special purposes, it is the non-conforming strains that will be worth looking for.

In describing a strain and forecasting its probable agronomic usefulness all characters studied have to be taken into con-

sideration. It is a matter of convenience to classify strains into groups of similar type and the obvious prime character on which to base a classification is relative time of ear emergence. Description, assessment and classification are much facilitated by comparisons with well-known established strains grown alongside as controls.

## Acknowledgement

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# INTERNATIONAL REGISTRATION OF VARIETIES OF HERBAGE PLANTS

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Since it is the recognised duty of the Food and Agriculture Organisation of the United Nations to promise and facilitate international collaboration among all its member countries or, where appropriate, on a more limited regional basis, consideration has naturally been given to the possible role of the Organisation in recent developments concerned with the International Code of Nomenclature for Cultivated Plants and the national and international registration of varieties or cultivars of herbage plants. It is therefore appropriate that this Branch of FAO should attempt to state its views, in the first place with particular reference to herbage plants since they, being largely cross-fertilized, present the greatest difficulties in these respects. It should be noted that the Crop Production and Improvement Branch deals with annual and perennial agricultural and horticultural crops, including pastures and fodder crops, and also that the Forestry Division of FAO has already appointed an International Registration Authority for Poplars.

## International Code of Nomenclature

As far as the International Code of Nomenclature is concerned, FAO was requested in a letter of 10th October 1955 from Dr J. Lanjouw, General Secretary, International Union of Biological Sciences, International Bureau of Plant Taxonomy and Nomenclature, to take an active part in the preliminary discussions in respect of agricultural varieties, since it was thought that this would be a logical activity with which the Organization should be associated.

FAO was obliged to state at that time that its part should be restricted to proposing the names of agricultural specialists

who might be invited to serve on the preparatory committee or be associated with its activities, in order to ensure that the special problems arising in a wider range of crops might receive adequate consideration in the Code.

The names suggested were :—

| | |
|---|---|
| Dr F. E. Nijdam . | Institute for Research on Varieties of Field Crops, Wageningen, Netherlands. |
| Dr R. Mayer . . | Station centrale de Genetique et d'Amelioration des Plantes, Versailles, France. |
| Dr P. S. Hudson . | Director, Commonwealth Bureau of Plant Breeding and Genetics, School of Agriculture, Cambridge, England. |
| A representative from | Division of Plant Industry of the United States Department of Agriculture. |
| Dr B. P. Pal . . | Director, Indian Agricultural Research Institute, Pusa, New Delhi, India. |
| Mr W. Hartley . | Principal Plant Introduction Officer, Division of Plant Industry, C.S.I.R.O., P.O. Box 109, City, Canberra, A.C.T., Australia. |

FAO was kept informed of developments, but the pressure for the Organization to undertake wider responsibilities nevertheless continued, particularly through the Sub-Commission on Agricultural Research of the European Commission on Agriculture. At the Third Meeting of this Sub-Commission held in Paris from 8th-12th April 1957, the delegate from Spain presented a proposal for the preparation of registers of plant varieties. The Sub-Commission recognized that FAO and OEEC had made progress on the standardization of procedure and nomenclature with regard to the certification of herbage cultivars. After a thorough discussion it was agreed that to promote further development FAO should act as a Post Office for the collection and dissemination of national lists of recognised varieties to be supplied by member countries. The Sub-Commission expressed its regrets and concern that FAO had not found it possible to take an active part in the International Committee on Registration of Cultivated Plants, and asked FAO to reconsider its position in order to ensure that agricultural crops would be adequately covered in any discussions which might be held by the International Committee. The Sub-Commission felt that FAO should be permanently represented in this Committee.

At the Fourth Session of the Sub-Commission held in Copenhagen, 23rd-27th September 1958, the delegate from Spain stated that he was pleased that FAO was now taking an interest in this question, and expressed satisfaction that the matter had been carefully considered. The Sub-Commission concluded that the work of FAO should be restricted to continuing to maintain contact with the International Committee on the Registration of Plant Varieties and to encouraging member countries to send to FAO lists of varieties as proposed at the Third Meeting of the Sub-Commission on Agricultural Research in Paris. The Sub-Commission approved of the activity of FAO in this field and requested that work be continued in order to ensure that adequate attention would continue to be given to agricultural crops.

The question has arisen at various times whether the agricultural part of the published Code was subject to sanction by the Organization, and whether and when that sanction was going to be given. Sanction of any such international document by FAO implies acceptance by its member countries at one of the biennial sessions of its Conference (1959, 1961 and so on). The procedure would probably be that the Crop Production and Improvement Branch would submit the Code with its preliminary comments to an international specialist group or groups in agriculture and horticulture (fruits and vegetables) by correspondence, and/or at a meeting in Rome or another centre, and/or at an international congress, such as, for example the 8th International Grassland Congress in 1960. The recommendations of these groups or conferences would then have to be referred back to the International Commission for the Nomenclature of Cultivated Plants. Ultimately an agreed revised version of the Code would be submitted with an explanatory background paper to the FAO Conference for approval and thus for formal acceptance by member governments. Already the Branch sees certain limitations in the existing Code with regard to herbage plants. It is felt that it was apparently designed in the first place for plants which are usually reproduced clonally. It may perhaps also be applicable to self-fertilized crops, but more difficult to apply to cross-fertilized crops such as many of the herbage and fodder crops. There are also certain details of wording that are of doubtful application. These are, however, matters which can be dealt with by the above-mentioned specialist groups containing

representatives from different countries and a range of ecological conditions, and are not our concern at the present time.

### International Registration of Cultivars (Varieties)

What is the purpose and desirability of an international registration of cultivars ? It could be useful in two different ways :—

(1) for registering names of new varieties in order to prevent the same name being given to different varieties, and to ensure that new names given are in accordance with the rules laid down by the International Code of Nomenclature ;

(2) for providing information about varieties, to provide breeders with lists of varieties suitable for different ecological conditions, and the addresses of institutions from which they could obtain seed of the desired varieties.

Registration of names of new varieties on an international basis is highly desirable for the international seed trade as well as for breeders, and such a registration would be necessary if breeders' rights were to be protected through some international patent law. For such a registration to be effective it is necessary that, before a name is published or officially given to a variety, it be approved by a registering authority. This authority would keep a complete list of varietal names which should include the names of all new varieties, of all varieties already on the market, and as far as possible, of older varieties which have already disappeared from common use.

Such an international registering authority would have to rely entirely on information given by the breeders or official authorities from the country of origin and it could in no case be responsible for a judgement on the agricultural value or the originality of the variety. In order to avoid as far as possible the adoption by different seed firms of different names for the same variety, the information listed in Appendix I of the Code of Nomenclature would be required with the application for registration, namely :—

(*a*) The name and nationality of the originator or introducer.

(*b*) The name of the describer or namer when the cultivar (variety) has been previously described or named.
(*c*) The name of the owner of the parental plant of a new budmutant (sport).
(*d*) The year in which the name was registered or published.
(*e*) The parentage when known.
(*f*) Particulars of testing.
(*g*) Awards received, with dates.
(*h*) A description in English, French, German, Russian or Spanish including, where applicable, details or colour (with reference to colour chart used), classification, chromosome data, etc.

The collection of information in order to be in a position to provide breeders with a list of varieties could be fairly restricted and comprise names of varieties from different countries and names of breeders or institutions keeping seed of these varieties. For that purpose, information given in the name register would be sufficient but naturally such a list could also be produced without an official registration of the variety. This list could also be enlarged to give information on the different characters of all listed varieties. This information could be more or less detailed, providing only a very general description of the variety, or very detailed information on morphological and physiological characters, somewhat similar to the FAO World Catalogues of wheat and rice. Naturally it would be very interesting and perhaps sometimes also useful to have all these details collected for herbage plants as well, making it possible for breeders to select breeding material with known characters from all parts of the world. To compile such descriptive lists would, however, be very laborious and involve many difficulties, and it is doubtful if the result would, in reality, have more than an academic interest. As most of the species used as herbage plants are cross-pollinated, the " cultivars " or " varieties " cannot be anything approaching pure lines, but rather populations composed of heterozygous plants ; it is not possible to give a reliable detailed description of such a " variety." Further, many of these populations are very sensitive to changes in environmental conditions, and their agricultural value and also their morphological characters will change considerably due to natural selection after a few genera-

tions of multiplication outside the district of origin. Finally according to the breeding system adopted in several countries, breeders intentionally make successive changes in their varieties in order to improve them without changing their names. This means that a description for a given name that is true to-day might not be true in a few years. Even without taking all these difficulties into consideration, it is felt that the need and usefulness of an international list giving detailed descriptions of herbage plant varieties are not great enough to justify the cost and work that would be involved.

## The possible role of FAO

As has been pointed out, registration of names of varieties on an international basis and the issue of a World List of Herbage Plant Varieties would be highly desirable. These activities certainly fall within FAO's field of activity, and of the international organizations now in existence none seems to be better suited to do the job than FAO. The degree to which FAO can or cannot undertake these activities will, however, depend entirely upon the costs and manpower involved and the ways in which the work could be financed. There are several alternative ways in which FAO might conceivably act with regard to the registration and/or the preparation of registers of herbage and fodder varieties and it is appropriate to discuss briefly the nature and possibility of these various projects :—

(1) FAO acts merely as a Post Office, collecting the national registers which countries, following agreement at a session of the FAO Conference, would be obliged to provide, and distributing these among the national registration authorities.

(2) FAO publishes a list of international and national registration authorities concerned with crop and horticultural plants in order to promote an interchange of correspondence.

(3) FAO acts as a registering authority for the names of cultivars (varieties).

(4) FAO collects national registers and compiles and publishes them into a consolidated whole progressively on a crop basis.

(5) FAO maintains a punch-card index of all registered varieties in order to be able to answer enquiries regarding specific crops with specific characteristics.

It would be possible for FAO to act as a Post Office as suggested in point (1); such an undertaking could be dealt with by the present staff without much extra cost. It is, however, questionable if there is any need for such centralized distribution of these national registers. It would probably be quite as efficient if FAO published a list of the authorities in the different countries responsible for the national registers and if institutions, plant breeders and other interested parties, requested the registers from those countries in which they were interested, either direct or through their own national authorities. Such a list provided by FAO could easily be extended to include other authorities mentioned under point (2).

The situation would be completely different if FAO were to act as an international registering authority. In that case, the project must be presented to the FAO Conference and adopted by the member countries. Furthermore such registration will involve so much work that it cannot be undertaken by the personnel now available. It must also be clearly pointed out that, if FAO should undertake the responsibility for the registration of the names of varieties, that responsibility must be limited to the registration of the *names* and should not by any means indicate any international recognition or authenticity of the *varieties*. An official recognition of varieties by FAO is impossible. It is probably correct to say that these national registers which have so far been established have different legal or regulatory bases, different standards of recording and reporting, and perhaps different levels of scientific accuracy. FAO could obviously not accord international recognition to varieties registered on such variable bases.

For these reasons and also because of the variable behaviour of herbage varieties at different localities, FAO would require a special field staff working at a network of stations observing the local behaviour of cultivars—a quite impossible objective. All responsibility for the material behind the name, the agricultural value, the originality and the maintenance of the variety must be placed entirely on the national bodies of the

country of origin, and therefore all applications for registration would have to be forwarded by these national authorities. In this connection it must also be emphasized that, even if FAO would take on the registration of the names, it will not be possible for the Organization to undertake the national protection of new varieties in connection with plant breeders' rights. It would be desirable that a list of these cultivars (varieties) included in the main International registry should be published on the lines indicated in Appendix 1 of the Code, as follows :—

" Registering authorities should compile and publish lists of cultivars' (varieties) names. This list should include :

(*a*) the names of the cultivars (varieties) in cultivation, giving for each the name and particulars enumerated above ;
(*b*) the names of all the cultivars (varieties) which, although no longer cultivated, are of historical importance—*e.g.*, as ancestors of existing cultivars (varieties).
(*c*) all known synonyms."

The mount of material being produced for publication by Crop Production and Improvement Branch is already in excess of the budget available for editing, translating into other official languages, and printing. Any cost for such a publication which is perhaps better called an Index than a Register, has therefore to be covered by outside sources. An indication of the time, labour and expense involved has been obtained through the preparation by Miss M. Hall of Bulletin No. 39, " 500 Varieties of Herbage Plants " published by the Commonwealth Bureau of Pastures and Field Crops, the FAO catalogues of Genetic Stocks, and the new FAO publication " A tabulated List of Tropical and Sub-Tropical Grain Legumes," prepared by Mr Y. T. Mao of this Branch.

Even if FAO does not assume the responsibility for the official registration of varietal names, it can still, with the reservation regarding staff and publication costs, collect information from national registering authorities and provide a publication as mentioned in No. 4 of the list of possible activities. To extend this to include detailed descriptions or to compile a punch-card index as suggested in point (5) does not seem, for the moment, to be sufficiently useful to justify the costs involved.

It is frequently thought that FAO is a mammoth international organization with ample funds and staff for the conduct of its work. In this connection, it is appropriate to mention that the staff of the Crop Production and Improvement Branch consists of 13 specialist officers. This Branch, together with Crop Protection Branch comprises the Plant Production and Protection Division of FAO. These officers have to deal with all crops through 76 member countries of the Organization as well as to undertake the responsibility for the technical guidance of regional staff and the 60 or more field officers working in the under-developed countries. It has to be stated that it would be impossible to undertake any of the objectives referred to above, no matter how desirable they may be, within the existing staff and budget. Special provision from an outside source would be necessary over and above the normal budget agreed upon at the biennial session of the FAO Conference. To deal with registration of varietal names, it would be necessary to provide for a specialist officer plus secretary plus travel for the officer, or approximately $20,000 per year. Any publication arising from the activities of this officer would not be covered in the FAO budget and would therefore be an additional charge. Such an officer could deal with herbage and fodder crops in the first instance, and he could :—

(*a*) compile lists of national registration authorities and maintain contact with them ;
(*b*) stimulate member countries to establish national registrations ;
(*c*) establish the specialist groups to consider the Code ;
(*d*) prepare conference documents ;
(*e*) be responsible for the registration and approval of new names of varieties.

Even if a start could be made with the herbage and fodder crops, this officer would fairly soon have to turn to other major groups of crops and deal with them in a way thought to be appropriate for that group, which may not necessarily be on the pattern suitable for herbage plants.

The standardization of national techniques, standards and procedures, a very desirable sequel to the work outlined in this article, is also an appropriate activity for FAO. This task,

which would be very great indeed, would involve obtaining international agreement on the techniques to be followed for the different groups of crops with all their different characteristics and requirements, and ensuring their adoption by member countries.

# SAMPLING FOR GENECOLOGY

D. A. Wilkins

Of the many techniques used by genecologists that of the garden trial was not only one of the earliest but seems likely to remain the most important. Such a trial is usually treated by means of the analysis of variance, but great care is needed in drawing biological conclusions from the discovery of statistically significant differences. In particular these conclusions depend on the nature of the error item used. If a descriptive result is all that is required, it being sufficient to show that two local populations or geographical races differ in genetic constitution, the ordinary "within population" or "within race" variance may be quite satisfactory.

The genecologist is usually not content with description, but seeks to relate the variation to selective factors in the environment. The problem is to distinguish between the results of selection and drift, using the latter term to cover all variation in gene frequency which is random with respect to the environment (Dobzhansky and Pavlovsky, 1957; Wright, 1949), and as random processes cannot be studied directly this entails eliminating drift in order to examine selection.

For this purpose the variance found within isolated local populations seems of little value. Even though such a population is large at the time of study there is every chance that it originated from a small number of colonisers, and so is likely to show drift differences from other populations. These differences would be expected even if the habitats were identical and when the habitats are different there seems no way of separating the adaptive differences from the drift differences on which they are superimposed.

The case of two geographical races is similar. The possibility that one was colonised by a small invasion from the other cannot be ruled out, and so any adaptive differences are again confounded with random ones to an unknown extent.

If it is desired that any significance found in an analysis should be attributable to selection—either in situ or via the selective migration of pre-adapted races—these effects of drift must be eliminated. When samples from several habitats are to be compared those habitats must occur mixed up in the same area, so that ecological and geographical differences are not

confounded. This is a difficult situation to define, and will vary with the species chosen, but the habitats must be so distributed that non-adaptive characters would be expected to vary at random among them. The second requirement is that the variance "within habitats" used for assessing the differences between them must not be that between the individuals of a local population. It is essential that the error variance should be "between populations within habitats." For a given size of trial the most representative possible sample from each habitat type is clearly obtained by increasing the number of population samples at the expense of their size. A sample of one individual from each site would ensure that the error variance was automatically that within a purely statistical assemblage of unrelated individuals. There would be no reason to expect any two such assemblages from the same geographical area to show non-adaptive differences.

Sometimes the purpose of a trial is not as clear-cut as this. Although the analysis of differences between a number of predetermined types of habitat remains the chief object it may be desirable to collect material which can be analysed later in a number of different ways. In such a case a compromise might be preferred. Strikingly aberrant populations, for example, might be overlooked completely if each were represented by only a single individual. It might then be better to collect a number of individuals from each population in order to get a better estimate of its mean. With the total number of plants in the trial limited by the usual practical considerations this would entail a reduction in the number of populations sampled, so that each habitat type was less well represented, and this gain of one kind of information at the expense of another must be recognised in the statistical analysis. The differences between habitats would still be compared with the variance between populations within habitats, and the degrees of freedom lost by reducing the number of populations would have to be transferred to an additional item for the variance between individuals within populations. This latter figure could be used for testing the significance of the differences between populations within habitat type, but such a test would be open to the objections already discussed, in that the differences could be due to an unknown combination of selection and drift.

Parts of this argument will be recognised as being similar to

that advanced by Harberd (1957, 1958). He was concerned with the special case of the vegetative spread of single genotypes and their consequent duplication in vegetative samples from small areas. It is suggested that what he called " spurious significance " is one result of a general uncertainty about the variance found within a local population. The standard error of the mean derived from that variance cannot be easily related to the expected differences between populations means. As in the case of genetic drift a sample with reduplication genotypes appears to be in some sense " too uniform." Whether reproduction is vegetative or sexual the extreme situations clearly have a lot in common. On the one hand there is a population made up entirely of genetically similar ramets of a single vegetative individual, and on the other one derived from the self-fertilisation of a single sexual ancestor. If either is treated as if it were a large population of genetically independent individuals it is likely to show a standard error which is too low with respect to the differences between populations. In less extreme cases, involving a number of vegetative genotypes or a number of sexual ancestors, the situation may not be quite so bad, but there seems little doubt that the variance within any local population is likely to be unpredictable and often composite in nature.

All that has been said so far concerns the analysis of variance, and the conclusions which can be drawn from the discovery of significant differences between groups of populations in a garden trial. If a range of values of a measurable habitat factor is available, instead of just a number of more or less arbitrary habitat types, it becomes possible to estimate the actual correlation of a plant character with the factor. Being independent of any particular system of classification of ecological " types of habitat " this is in some ways a more objective method of measuring genecological relationships. We are not concerned here with the admitted difficulties of choosing likely factors and characters to measure, but only with the collection of material and the interpretation of the results, and the precautions needed are very similar to those already discussed for the analysis of variance.

The chief danger lies in a well-known property of correlation statistics. Two characters may be measured in each of two populations and found to be uncorrelated. If, however, the means of the populations differ in both characters the mixing

together of the two sets of figures will automatically produce a correlation. When only two populations are involved the situation is clear, as there is no correlation within the populations and there can be no question of having a correlation between only two means. The apparent correlation obtained by mixing the two sets has no meaning, and does not call for a biological interpretation. Increasing the number of populations from two to four makes it possible to calculate one correlation co-efficient between their means, which can be tested for significance on the basis of the two or three degrees of freedom available, and another to represent the average correlation within the populations. If neither of these is significant it may still be possible to obtain a significant correlation by pooling the results and ignoring the fact that they come from different populations. The analogy with the two-population case suggests that this overall correlation cannot be interpreted, and attention must be confined to its two components even when they are of lesser significance.

If one individual is collected from each local population, as suggested earlier, and a habitat measurement obtained from each site, there is only one correlation coefficient and so no ambiguity. There seems little doubt that a significant correlation of this kind can only be accounted for in terms of adaptive genetic differences. It cannot be assumed that the actual character and factor measured are directly related themselves, as in either case it might be that the choice of a related character or a related factor would have given an even higher correlation, but the conclusion that some genetic difference between the plants is adapted to some difference between the habitats seems inescapable.

If several individuals are collected from each local population and a separate habitat measurement is available from the actual point of collection of each plant, the factor and character may be correlated at two levels—within and between populations. The interpretation of a correlation within a breeding population needs great care. In the rare cases where there is free gene dispersal over the area, so that it can be assumed that each gene has equal access to every gradation of the habitat factor, the correlation must be due to selection. On the other hand any process such as vegetative spread which leads to dispersal over a small part of the area, and so probably into only a restricted range of the factor, could produce a misleading

correlation of the type discussed at the beginning because of the pooling of heterogeneous figures. A correlation within a local population seems to be just as difficult to interpret as the within population variance, and for closely similar reasons.

The correlation found between population means, by comparison, is much more informative, having exactly the same properties as those already discussed in the case of a single plant from each population. As long as the populations are not collected from two or three distinct regions which may show random differences, the only interpretation seems to be in terms of adaptation and selection.

It is recognised that there are many practical difficulties in collecting material satisfying such requirements as these. The detection of the limits of a breeding population and the assessment of its degree of isolation from the next are often extremely difficult, and even in theory these may not be clear-cut but vague and fluctuating. A small number of gametes may each year be spread over the whole area studied, and yet some of the local populations may remain relatively isolated and self-sufficient. Such things make the collection of suitable material even more difficult, but they do not affect the main argument which has been advanced—that the differences between two groups cannot be assumed to be adaptive if the individuals within a group are more closely related than are those in different groups. Because of this it is always desirable to take small samples from a large number of isolated sites rather than large samples from fewer sites, and to avoid any marked degree of geographical separation between the groups of sites compared, and it makes no difference to this whether the species is vegetative, inbreeding, or outbreeding in its reproduction.

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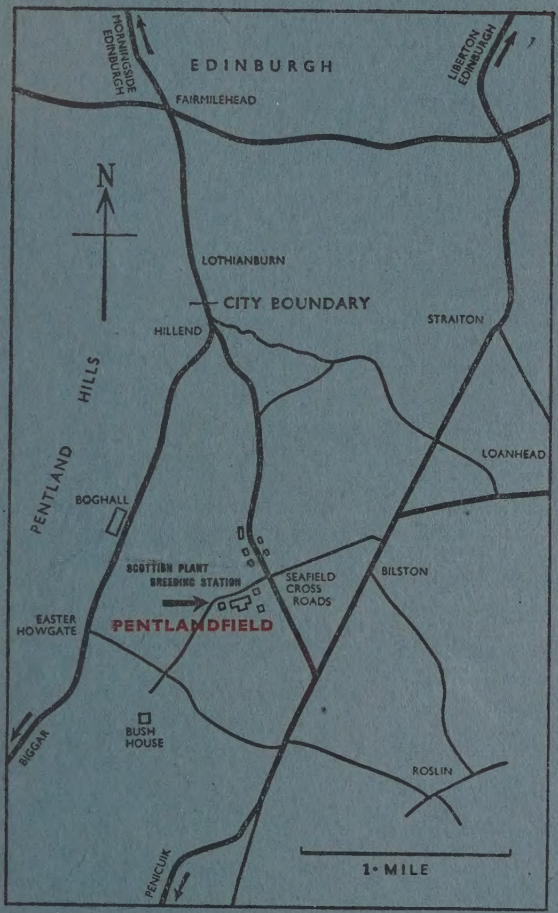
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